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Republic of South Africa
Department of Industries
Sea Fisheries Branch

JUL 18 1978

FISHERIES BULLETIN

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CONTRIBUTIONS TO OCEANOGRAPHY AND FISHERIES BIOLOGY

Cape Town

1978

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Published in 1978 by the Sea Fisheries Branch, Beach Road, Sea Point 8001, Cape Town.

Fish. Bull. S. Afr. 10:1–88

ISBN 0 621 03762 1

Edited by
H. G. v. D. Boonstra
and
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(Hierdie uitgawe is ook in Afrikaans gratis van die Tak Seevisserye verkrygbaar.)

Printed for the Government Printer, Pretoria,
by
Galvin & Sales (Pty) Ltd, Cape Town.

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Fish. Bull. S. Afr. 10:1–9
1978

ALLELE COMBINATIONS RESPONSIBLE FOR HETEROZYGOTE DEFICIENCY IN ESTERASE POLYMORPHISM OF THE PILCHARD *SARDINOPS OCELLATA*

F. LE CLUS

Single locus polymorphism can be used as a marker gene for populations, stocks and races (Gooch 1975) but is unreliable as the key indicator if it does not conform to the Hardy-Weinberg law (Fujino 1971). The Hardy-Weinberg law of genetic balance states that in a randomly mating population, in the absence of a variety of disturbing forces (e.g. selection, mutation), the expected distribution of genotypes is determined by the random combination of alleles (Utter *et al.* 1974). In the case of two alleles, A and B, expected genotypic frequencies are:

Genotype	AA	AB	BB
Frequency	q^2	$2q(1-q)$	$(1-q)^2$

where q is the portion of A alleles in the population.

With electrophoretic techniques, the position of a specific enzyme is determined by appropriate staining of the gel. The position of the enzymes depends upon the genetically determined electrophoretic mobility of the protein. A single band found in one specific zone of a gel for all individuals indicates that one locus in a chromosome pair is responsible for the enzyme and that the whole population is monomorphic for that enzyme. If two bands occur in the same zone in some individuals and single bands in either position in other individuals, two different alleles on the same locus of a chromosome pair can be deduced. This population is polymorphic for the enzyme. Sometimes in each individual of the population, more than one locus on the chrosome pairs produces the enzyme but with slightly different molecular configuration (isozymes), so that for each individual the isozymes are found in more than one zone in the gel.

In the esterase system of the pilchard *Sardinops ocellata,* six zones of activity were found in the gels (Thompson and Mostert 1974), but of these only three zones appeared in sufficient strength to be easily identifiable. Initial work concentrated on the polymorphic zone II where eleven bands were distinguished. The alleles responsible for these bands were labelled A to K in decreasing order of electrophoretic mobility of the allelic variants. The K allele was not recorded in the 500 fish used in the present study.

Thompson and Mostert (1974) compared the zone II esterase allele frequencies of fish from three areas round the coast of southern Africa. The allele frequencies of each area differed significantly from the expected frequencies derived from the combined values. This suggested the possibility of separate stocks. However, heterozygote deficiency indicating genetic imbalance was present in each area. Therefore, the differences between the areas could have been the result of disturbing forces other than genetic isolation of the stocks.

In the present report, an attempt is made to isolate specific factors or alleles responsible for heterozygote deficiency.

MATERIAL AND METHODS

Five batches of 100 adult pilchards were analysed. They were collected near Walvis Bay (between 22°10′S and 22°30′S) over a short period between 3 and 10 April 1973 (Table I).

The five batches were expected to have the same allele frequency distribution. Four of the batches, however, differed significantly from the expected frequency derived from the combined values. Heterozygote deficiency was present in every batch. Males and females were then analysed separately in case differences in ratios within the batches were obscuring the results. In the same way, length groups and maturity stages were analysed separately (Table I).

The extraction of muscle tissue samples, the methods used in the horizontal, starch gel electrophoresis and the notation adopted for describing the esterase zone II results were as described by Thompson and Mostert (1974).

Table I: Details of pilchard samples collected

Batch	Position		Date: April 1973	Number of fish			
	Latitude	Longitude		Maturity stage 1		Maturity stage 3	
				Male	Female	Male	Female
1	22°10′S	14°00′E	3	0	10	24	66
2	22°20′S	14°18′E	4	8	21	36	35
3	22°10′S	14°08′E	5	12	23	31	34
4	22°25′S	14°00′E	9	42	27	16	15
5	22°30′S	14°10′E	10	2	22	34	42
Total				64	103	141	192

RESULTS

Allele frequency analysis

Once the allele frequency of each of the five batches had been determined, an attempt was made to establish whether the differences in the frequency distribution were statistically significant. If it is assumed that the five batches were drawn from a homogeneous population, the mean observed number of alleles may be taken to represent the expected number, p, for this population (Table II).

A contingency table was drawn up to test the numbers of alleles observed against those expected in the five batches. In the χ^2 tests the A, B, I and J allele types were grouped together, because the numbers expected were fewer than five (Snedecor and Cochran 1967). Four of the batches differed at a statistically significant level from the expected number (Table II).

When the allele types were tested separately, allele types C, D and E showed the biggest deviation from the expected number ($P < 0{,}001$). The allele frequencies of types F, G and H did not differ significantly from the expected values, thus indicating that only allele types C, D and E were responsible for the observed genetic imbalance. The allele types A, B, I and J were not tested owing to insufficient numbers.

Boundaries showing the minimum and maximum likelihood of occurrence of each allele type within a batch provided further information about the deviation of each observed allele number from the expected values derived from

Table II: Contingency table to test the number of alleles observed against those expected in the five batches

Allele type	Allele total	Expected number (p)	Observed number per batch					χ^2	Degrees of freedom	P
			1	2	3	4	5			
A	8	1,6*	2	4	0	2	0	—		
B	19	3,8*	2	3	7	4	3	—		
C	84	16,8	8	8	35	10	23	33,98	4	< 0,001
D	237	47,4	10	61	50	46	70	44,37	4	< 0,001
E	327	65,4	93	57	46	80	51	24,91	4	< 0,001
F	153	30,6	43	25	34	22	29	8,93	4	+
G	117	23,4	28	29	18	22	20	4,07	4	+
H	45	9,0	7	12	8	14	4	7,11	4	+
I	9	1,8*	6	1	2	0	0	—		
J	1	0,2*	1	0	0	0	0	—		
χ^2			53,89	13,00	27,70	11,60	22,06			
Degrees of freedom			6	6	6	6	6			
P			< 0,001	< 0,05	< 0,001	+	< 0,001			

\+ No significant deviation from expected values
* Expected numbers fewer than five were added together

Table III: Allele frequency distribution and the minimum and maximum likelihood of occurrence of the alleles for the combined total of the five batches

Allele type	Mean allele frequency (p)	95% pignic probability (2 x standard deviation of p)	Likelihood boundaries	
			Minimum	Maximum
A	0,008	0,0056	0,5	2,7
B	0,019	0,0086	2,1	5,5
C	0,084	0,0176	13,3	20,3
D	0,237	0,0268	42,0	52,8
E	0,327	0,0296	59,5	71,3
F	0,153	0,0228	26,0	35,2
G	0,117	0,0204	19,3	27,5
H	0,045	0,0132	6,4	11,6
I	0,009	0,0060	0,6	3,0
J	0,001	0,0020	0,0	0,6

the combined batches. The probable standard deviation of the expected frequency (σ_p) was calculated from the equation (Smith 1969, p.377):

$$\sigma_p = \left[\frac{ab}{(a+b)^3}\right]^{\frac{1}{2}}$$

where a represents the observed number of chromosomes with the y allele and b represents the number of chromosomes with alleles other than y. The limits of the 95 per cent pignic probability were obtained by doubling the standard deviation (SD). Minimum and maximum likelihood of occurrence of allele y was derived by respectively subtracting or adding 2 x SD from the mean frequency of each allele and multiplying by 200, the total number of alleles per sample (Table III). The allele number of each batch was then examined to determine whether it fell inside or outside the minimum/maximum likelihood boundaries (Table IV). It was found that, in many cases, 99 per cent pignic probability was exceeded (3 x SD). The number of chromosomes with C and E alleles was outside 99 per cent pignic probability in all batches except the E allele in batch 2 which was outside 95 per cent pignic probability.

Data for Gans Bay (34°40′S, 19°20′E) and Ambrose Bay (21°06′S, 13°04′E) provided by Thompson and Mostert (1974) were also compared with the minimum/maximum boundaries of the present study. The Gans Bay data fell outside the boundary for 99 per cent pignic probability in 7 of the 10 allele types. From Ambrose Bay, the same probability boundary was exceeded in 6 of the 10 allele types, a similar deviation to that found in batch 1, but a higher one than those of the other four batches studied (Table IV).

The differences in allele frequencies found between the five batches during the present study could not be ascribed to different ratios of the sexes or of maturity stages 1 and 3, nor to the variable number of fish within the length groups.

Separate tests were conducted on male and female fish of maturity stage 3. For each sex, the allele frequency was first determined from the total distribution of alleles. In the case of females, numbers were sufficient for further comparison in four length groups, but in the case of males only two length groups could be studied. No significant differences between expected and observed numbers of alleles were found either within or between the 1-cm length groups of either sex (Tables V and VI).

When tests were made between the allele fre-

Table IV: Allele frequencies within each batch of pilchards that fell inside or outside the minimum/maximum likelihood of occurrence boundaries

Allele type	Batch					Ambrose Bay*	Gans Bay*
	1	2	3	4	5		
A	×	++	++	×	++	×	×
B	×	×	++	×	×	++	×
C	++	++	++	++	++	++	++
D	++	++	×	×	++	++	++
E	++	+	++	++	++	++	++
F	++	+	×	++	×	×	×
G	+	+	+	×	×	×	++
H	×	+	×	++	++	++	++
I	++	×	×	+	+	×	++
J	++	×	×	×	×	++	++

* After Thompson and Mostert (1974)
× Inside boundaries
\+ Outside boundaries (95% pignic probability)
++ Outside boundaries (99% pignic probability)

Table V: Contingency table to test the number of alleles observed against those expected for different length groups of males in maturity stage 3

Allele type	Mean allele frequency**	Total length groups				χ^2	Degrees of freedom	P
		23 cm		24 cm				
		Observed	Expected	Observed	Expected			
A	0,0071	1	1,0*	1	0,7*	—		
B	0,0284	2	4,0*	5	2,7*	—		
C	0,0922	12	13,1	12	9,0	1,09	1	+
D	0,1695	38	38,3	27	26,4	0,02	1	+
E	0,2979	46	42,3	27	29,2	0,49	1	+
F	0,1454	21	20,6	11	14,2	0,73	1	+
G	0,0957	12	13,6	10	9,4	0,23	1	+
H	0,0461	10	6,5	3	4,5*	—		
I	0,0177	2	2,5*	2	1,7*	—		
χ^2		3,33		2,14				
Degrees of freedom		6		5				
P		+		+				

\+ No significant deviation from the expected numbers
* Expected numbers fewer than five were added together
** Allele frequency of all males in maturity stage 3

quencies of males and females (all length groups combined), no significant differences from the expected values were found for either maturity stages 1 or 3 (Tables VII and VIII). The same negative result was obtained when males and females were combined and maturity stages 1 and 3 tested for deviation from the expected (Table IX). In all instances, the expected frequencies were derived from the combined values of the groups tested.

Table VI: Contingency table to test the number of alleles observed against those expected for different length groups of females in maturity stage 3

Allele type	Mean allele frequency**	Total length groups								χ^2	Degrees of freedom	P
		23 cm		24 cm		25 cm		26 cm				
		Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected			
A	0,0052	2	0,4*	0	0,8*	0	0,6*	0	0,2*	—		
B	0,0130	0	1,0*	3	2,0*	1	1,4*	1	0,5*	—		
C	0,0729	6	5,4	13	11,1	6	8,0	3	2,8*	0,91	3	+
D	0,2344	21	17,3	37	36,0	24	25,8	7	9,0	1,39	3	+
E	0,3724	25	27,6	46	56,6	49	41,0	19	14,2	5,41	3	+
F	0,1484	9	11,0	27	22,6	16	16,3	4	5,6	1,68	3	+
G	0,1094	10	8,1	18	16,6	10	12,0	3	4,1*	1,19	3	+
H	0,0339	1	2,5*	6	5,2	3	3,7*	1	1,3*	—		
I	0,0104	0	0,8*	2	1,6*	1	1,1*	0	0,4*	—		
χ^2		2,53		3,52		3,00		2,71				
Degrees of freedom		5		6		5		3				
P		+		+		+		+				

\+ No significant deviation from the expected numbers
* Expected numbers fewer than 5 were added together
** Allele frequency of all females in maturity stage 3

Table VII: Contingency table to test the number of alleles observed against those expected for males and females in maturity stage 1

Allele type	Mean allele frequency			Male		Female		χ^2	Degrees of freedom	P
	Male	Female	Combined	Observed	Expected	Observed	Expected			
A	0,0156	0,0097	0,0126	2	1,6*	2	2,6*	—		
B	0,0156	0,0194	0,0175	2	2,2*	4	3,6*	—		
C	0,0859	0,0922	0,0890	11	11,4	19	18,3	0,05	1	+
D	0,2031	0,2184	0,2107	26	27,0	45	43,4	0,00	1	+
E	0,3125	0,2913	0,3019	40	38,6	60	62,2	0,13	1	+
F	0,1641	0,1650	0,1645	21	21,1	34	33,9	0,00	1	+
G	0,1328	0,1505	0,1416	17	18,1	31	29,2	0,18	1	+
H	0,0703	0,0485	0,0594	9	7,6	10	12,1	0,65	1	+
I	—	—	—	—	—	—	—	—		
J	0,0000	0,0049	0,0025	0	0,3*	1	0,5*	—		
χ^2				0,43		0,68				
Degrees of freedom				6		6				
P				+		+				

\+ No significant deviation from the expected numbers
* Expected numbers fewer than 5 were added together

Genotype analysis

According to the Hardy-Weinberg law, the expected number of fish can be determined from allele frequencies for all the homozygotes and for all possible combinations of heterozygotes. For each batch of pilchards collected, as well as for males and females in maturity stages 1 and 3, this calculation was performed. In every instance, the number of homozygotic fish was about double the expected number (Table X) with a concomitant heterozygote deficiency. For each homozygotic genotype, the number of fish observed varied considerably between batches (Table XI). This variation indicated that the factor responsible for the genetic imbalance was not constant for all the batches.

The heterozygote deficiency was analysed for the batches combined to establish which heterozygotes were involved. It was found that of 45 possible heterozygotes only four were implicated in the deficiency (Table XII). The heterozygotes

Table VIII: Contingency table to test the number of alleles observed against those expected for males and females in maturity stage 3

Allele type	Mean allele frequency			Male		Female		χ^2	Degrees of freedom	P
	Male	Female	Combined	Observed	Expected	Observed	Expected			
A	0,0071	0,0052	0,0062	2	1,7*	2	2,4**	—		
B	0,0284	0,0130	0,0207	8	5,8	5	7,9	—		
C	0,0922	0,0729	0,0825	26	23,3	28	31,7	0,74	1	+
D	0,2695	0,2344	0,2520	76	71,1	90	96,8	0,81	1	+
E	0,1979	0,3724	0,3351	84	94,5	143	128,7	2,76	1	+
F	0,1454	0,1484	0,1469	41	41,4	57	56,4	0,01	1	+
G	0,0957	0,1094	0,1026	27	28,9	42	39,4	0,30	1	+
H	0,0461	0,0339	0,0400	13	11,3	13	15,4	0,63	1	+
I	0,0177	0,0104	0,0141	5	4,0*	4	5,4	—		
χ^2				3,33		4,53				
Degrees of freedom				7		7				
P				+		+				

\+ No significant deviation from the expected numbers
* Expected numbers fewer that 5 were added together
** The expected number fewer than 5 is omitted

Table IX: Contingency table to test the number of alleles observed against those expected for all pilchards in maturity stages 1 and 3

Allele type	Mean allele frequency			Stage 1		Stage 3		χ^2	Degrees of freedom	P
	Maturity stage 1	Maturity stage 3	Combined	Observed	Expected	Observed	Expected			
A	0,0119	0,0060	0,0089	4	3,0*	4	5,9*	—		
B	0,0179	0,0195	0,0187	6	6,2	13	12,5	0,03	1	+
C	0,0898	0,0810	0,0854	30	28,2	54	56,9	0,26	1	+
D	0,2025	0,2492	0,2259	71	75,5	166	150,4	1,89	1	+
E	0,2894	0,3408	0,3201	100	106,9	227	213,1	1,34	1	+
F	0,1646	0,1471	0,1559	55	52,1	98	102,8	0,49	1	+
G	0,1437	0,1036	0,1237	48	41,3	69	82,4	2,90	1	<0,05
H	0,0568	0,0390	0,0479	19	16,0	26	31,9	1,65	1	+
I	0,0000	0,0135	0,0068	0	2,3*	9	4,5*	—		
J	0,0029	0,0000	0,0015	1	0,5*	1	1,0*	—		
χ^2				2,76		9,11				
Degrees of freedom				7		8				
P				+		+				

\+ No significant deviation from the expected numbers
* Expected numbers fewer than 5 were added together

CE, DE, EF and CD were contributing 95 per cent of the significant χ^2 value for heterozygote deficiency. The combinations containing alleles A, B, G, H, I and J complied with the Hardy-Weinberg law for genetic balance as did all heterozygotes containing the F allele with the exception of EF.

DISCUSSION

Thompson and Mostert (1974) found significant differences in the zone II esterases of pilchards collected from three different areas. This suggested the possibility of separate pilchard stocks. However, in the present study pilchards collected within a short space of time and from the same area also showed significant differences between batches (Table II).

This was unexpected. A free flow of alleles in the population, in the absence of any disturbing forces, should not have resulted in statistically significant differences in allele frequencies of the five batches. Because physical and genetic isolation in the same area seemed improbable, these differences could have resulted from the heterozygote deficiency observed in all batches.

Many factors could have been responsible for

Table X: Contingency table to test the observed number of homozygotes and heterozygotes against those expected for genetic balance in a randomly mating population (Hardy-Weinberg equilibrium)

Batch		Homozygotes		Heterozygotes		χ^2	P*	Homozygote ratio
		Observed	Expected	Observed	Expected			
1		48	28,95	52	70,98	17,61	< 0,001	0,48
2		48	21,67	52	78,33	40,84	< 0,001	0,48
3		40	18,57	60	81,51	30,51	< 0,001	0,40
4		49	24,50	51	75,50	32,45	< 0,001	0,49
5		48	23,13	52	76,87	34,79	< 0,001	0,48
Female	stage 1	42	19,96	61	83,04	30,19	< 0,001	0,41
	stage 3	95	45,00	97	147,00	72,56	< 0,001	0,49
Male	stage 1	18	12,56	36	51,44	23,61	< 0,001	0,44
	stage 3	69	28,69	72	112,31	71,10	< 0,001	0,49

* One degree of freedom

Table XI: Observed and expected number of homozygotes within batches

Homozygote type	Expected number		Observed number					Total
	per 100	per 500	1	2	3	4	5	
CC	0,71	3,55	1	2	8	1	6	18
DD	5,57	28,10	0	16	11	13	20	60
EE	10,63	53,45	33	18	12	25	15	103
FF	2,40	11,70	9	3	8	6	5	31
GG	1,42	6,85	3	5	1	2	2	12
Others	0,64	3,20	2	4	0	2	0	8
Total	21,37	106,85	48	48	40	49	48	232

the heterozygote deficiency of zone II esterases in pilchards. It could have been linked with fish length, as was found for the mackerel *Scomber scombrus* from the southern part of the North Sea where only the 26–30 cm length group, which consisted mostly of one strong year-class, showed genetic balance (Jamieson *et al.* 1971). This could have been because the egg and larval stages are those most likely to be affected by selection pressure. Fish that cannot adapt to a wide range of environmental conditions tend to avoid those that are unfavourable (Gilles 1975), which their larvae cannot do. Because spawning conditions may vary from year to year, a difference in allele frequency between year-classes owing to differential selection pressures may result.

The heterozygote deficiency could have been sex-linked, as was found in the Pacific hake *Merluccius productus,* where the heterozygote deficiency of the esterase variants occurred in males only (Utter and Hodgins 1971). Also, it could have been linked with maturity stage. Because fish in different stages of maturity spawn at different times, differential environmental selection pressure would be exerted on the genome.

If a link had been found between heterozygote deficiency and factors such as length group, sex and stage of maturity, the significant differences in allele frequency between the five batches of pilchard could have been explained.

The heterozygote deficiency found in pilchard was not, however, linked with length group, sex or maturity (Tables V to IX) but with four specific heterozygotes (CE + DE + EF + CD). These four heterozygotes accounted for 95 per cent of the statistically significant χ^2 value (Table XII). The individual alleles C, D, E and F do not themselves have reduced fitness because in that case they would have been lost from the gene-pool of the population. The four alleles comprised 80,5 per cent of the total number of homozygotes, but their heterozygotes only 23,5 per cent of the total number of heterozygotes. These values suggest that selection against these heterozygotes is taking place in the pilchard population.

An undetected "silent" allele may account for esterase heterozygote deficiency in the mysid *Mysis relicta* (Fürst and Nyman 1969). A "silent" allele is not expressed as a detectable enzyme and in the gel would give a single band equivalent to a homozygote. However, a "silent" allele

Table XII: Observed and expected numbers of homozygotes and heterozygotes for the combined batches

Genotype		Observed (O)	Expected (E)	$\frac{(O-E)^2}{E}$
Homozygotes		233	106,85	148,936
Heterozygotes	CE, DE, EF, CD	63	174,70	71,419
	DF, CF	53	49,60	0,233
	AC, BC, CH, CI, CJ	6	6,09	0,001
	AD, BD, DH, DI, DJ	13	17,96	1,385
	AE, BE, EH, EI, EJ	28	27,04	0,034
	AF, BF, FH, FI, FJ	10	12,21	0,400
	All with G allele	93	105,19	1,413
	Others	1	0,64	0,203

in the zone II esterase polymorphism of the pilchard would mean that combinations of the "silent" allele with alleles other than C, D and E could not occur, otherwise genetic balance would not have been possible for the other alleles as was found. The presence of a "silent" allele does not, therefore, offer an explanation for the heterozygote deficiency in pilchard.

Heterozygote deficiency seems to be a characteristic frequently encountered in connection with esterase polymorphisms. It has been found in such fish species as mackerel *Scomber scombrus* (Jamieson *et al.* 1971), the catastomid *Catastomus clarkii* (Koehn 1969), sprat *Sprattus sprattus* (Howlett and Jamieson 1971) and males of the Pacific hake *Merluccius productus* (Utter and Hodgins 1971). It has also been recorded in other groups of animals such as the echinoderm *Ophiomusium lymani* (Murphy *et al.* 1976, Doyle 1972) and the mysid *Mysis relicta* (Fürst and Nyman 1969).

However, not all esterase systems showed genetic imbalance. No significant deviation from the numbers expected was found for herring *Clupea harengus harengus* (Ridgeway *et al.* 1971), skipjack tuna *Katsuwonus pelamis* (Fujino 1971) or albacore *Thynnus (Germo) alalunga* (Serene 1971).

Before esterase polymorphism can be evaluated as a possible genetic marker for pilchard sub-populations, it is necessary to consider the effects of heterozygote deficiency on the stability of the polymorphic system.

In the case of heterozygote deficiency as a result of selection against the heterozygote, the stability of the polymorphism will be destroyed unless there is a recurrent shift to selection against the homozygotes (Gooch 1975).

Where polymorphism is maintained in spite of selection against the heterozygotes, environmental differences may influence the selection coefficients in such a way that one allele is favoured in some conditions and another allele in other conditions (Falconer 1964). For instance, heterozygote deficiency of the esterase system of the catastomid freshwater fish *Catastomus clarkii* was the result of the action of temperature as a selection agent (Koehn 1969). The heterozygote exhibited the greatest activity over the greatest range of temperature, but was exceeded in activity at both ends of the temperature scale by one or the other homozygote (Koehn *op. cit.*). Thus, heterozygosity was maintained within populations by overdominant selection relative to environmental temperature variation (Koehn 1971).

Not all protein heterogeneity is maintained by the selective action of temperature, but temperature could have a profound effect on many biochemical polymorphisms. All enzymes exhibit changes in catalytic properties with changes in temperatures (Koehn 1971). Enzymatic characteristics relevant to any environmental variable must exist as some optimal combination of maximum efficiency and maximum tolerance to environmental variation (Koehn *op. cit.*).

King (1977) showed that concentrations of pilchard eggs off South West Africa are closely related to surface water temperatures and that a distinct separation between north and south spawning groups can be made. No large concentrations of eggs were found in the southern area in water of surface temperature greater than 16,5°C or in the northern area in water of surface temperature lower than 16,5°C. These temperature regimes could exert a differential selection pressure which may explain the heterozygote deficiencies found.

Heterozygote deficiency would occur if larvae were recruited from several populations differing in allele frequency from their pooled genotype distribution – the Wahlund effect (Gooch 1975). Thompson and Mostert (1974) gave this as a possible explanation for the observed heterozygote deficiency in pilchard *Sardinops ocellata*. However, the existence of sympatric stocks or breeding units with distinctive allele frequencies and genetic balance has not yet been proved.

The zone II esterase polymorphism may not yet be useful as a key genetic marker for stock separation owing to the proven genetic imbalance. However, there may be some application. If selection pressures cause the imbalance, they may be constant for a stock or area and may give rise to stable allele frequencies for a particular stock (D. Thompson, Fisheries Laboratory Lowestoft, personal communication). For instance, in pilchards collected near Gans Bay, there were 61,7 per cent homozygotes other than CC, DD, EE or FF while near Walvis Bay only 8,6 per cent of the zone II esterase homozygotes were other than one of these four.

To summarize, analysis of zone II esterase polymorphism showed statistically significant differences between pilchards from three different localities around the southern coast of Africa. However, statistically significant differences were also found between five batches in the same area. The heterozygote deficiency found in all batches could have been responsible for the statistically significant χ^2 values. However, the zone II esterase polymorphism was due to only four heterozygotes (CD, CE, DE and EF) out of

a possible 45.

Owing to the heterozygote deficiency, zone II esterase polymorphism can not be used as a key genetic marker for pilchard stocks. To find key genetic markers, more loci will have to be examined for likely polymorphisms, larval stages should be typed as early in the life cycle as technically possible and material should be collected from as wide a geographical area as possible.

ACKNOWLEDGEMENTS

I would like to thank Dr D. Thompson and Mr S. Mostert for allowing their data to be incorporated in this report. Dr D. Thompson and Messrs A. A. Jackson, O. M. Centurier-Harris and R. J. M. Crawford are acknowledged for their constructive criticism of the manuscript.

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Fish. Bull. S. Afr. 10:10–14
1978

CHANGES IN THE RATE OF MORTALITY IN THE SOUTH WEST AFRICAN PILCHARD EVALUATED FROM TAGGING

R. M. THOMAS and F. H. SCHÜLEIN

The pilchard *Sardinops ocellata* supports an important industry in South West Africa. Recent research (Schülein *et al.* 1975) has shown that stock size has varied considerably over the last two decades. In 1956, a large-scale pilchard tagging programme was initiated in Walvis Bay and continued until 1966. Records of tags returned are available from 1958 to 1971. Although the primary purpose of this programme was to determine stock size – Newman (1970) considered the results of tag returns up to 1966 – it has also subsequently proved possible to determine from the records of tag returns how mortality rates have changed. The aim of the present report is to show, in a semi-quantitative manner, the magnitude of these changes. Similar studies were conducted by Hart (1943) and Clark and Janssen (1945) on the Pacific sardine. However, their methods omitted consideration of changes in the size of the exploitable stock or catch. This shortcoming is avoided here by the introduction of factors which eliminate changes in recruitment or catch from the results.

METHODS

Tagging was conducted during the closed season from October to January each year, a metal tag being inserted into the coelomic cavity of each fish. The closed season was selected for tagging in order to allow a certain amount of mixing and dispersal of the tagged fish throughout the population. Approximately 1 000 fish were tagged each week off Walvis Bay. Tags were recovered by means of magnets in the fish meal plants of the eight Walvis Bay factories and the single factory in Lüderitz. Newman (1970), in evaluating magnet efficiency tests carried out in 1965 and 1966 at the Walvis Bay factories, found an average efficiency of tag recovery of 75 per cent and 81 per cent respectively. Magnet efficiencies, sustained tagging mortalities and other loss coefficients are not known for the entire period, but it is assumed here that these remained relatively constant and that the results are, therefore, subject to a constant error.

Fish tagged within a given period were grouped and treated as a single cohort, easily identifiable by means of the serial numbers of the tags used. Five cohorts were selected for study as shown in Table I.

Annual tag returns per cohort from the Walvis Bay and Lüderitz factories were summed for each year, divided by the annual land-based pilchard catch and multiplied by the estimated biomass of the stock for that year to give an estimate of the number of tags per cohort in the stock:

$$N_t = \frac{n_t}{Y_t} \times B_t \qquad (1)$$

where

N_t = number of tags/cohort in the stock in year t,

n_t = number of tags/cohort returned in the catch in year t,

Y_t = annual land-based pilchard catch in year t, and

B_t = estimated biomass of the commercial stock in year t.

The use of this method requires that mixing is complete and that the number of tags in the catch is thus proportional to the number of tags in the commercial stock, a condition it was attempted to meet by tagging in the closed season only. Also, the ratio n_t/N_t would then remain constant for each cohort sampled in year t and be independent of recruitment.

$\text{Log}_e N_t - \log_e N_{t+1}$ is an estimate of the instantaneous rate of decrease in the numbers of tags per cohort in the commercial stock for one year (Z'), and can be divided into five coefficients:

$$Z' = F + M + M' + E + U \qquad (2)$$

Table I: Tagging details of the five selected cohorts

Tag serial numbers	Dates tagged	Cohort
A72450 – A79999	13/1/58–13/2/58	1957/58
B59690 – B68199	13/11/59–22/1/60	1959/60
B40000 – B48999	27/12/62–6/2/63	1962/63
C53000 – C61999	6/1/65–9/2/65	1964/65
D50000 – D59999	10/1/66–3/3/66	1965/66

where

F = fishing mortality,
M = natural mortality,
M′ = sustained tagging mortality,
E = loss due to emigration, and
U = "other loss" coefficient.

The annual Z′ values were treated in two ways:

(i) Least-squares regression lines were drawn through the N_t values to obtain an average Z′ per cohort. However, this method of lumping data masks any changes in Z′ which may have occurred in consecutive years (as indicated by Cram, in press).

(ii) For this reason, Z′ values from different cohorts were averaged to provide a value for each year. Where the number of tags returned (n_t) was less than ten, the corresponding Z′ values were not used to calculate averages.

Z′ is not affected by the initial tagging mortality, as this would clearly only determine the initial tag numbers in the stock and not the subsequent rate of decay. Initial tagging mortality is thus not considered further.

The present calculations are based on the annual land-based catch which is a very large sample of the stock and can therefore be considered as representative.

Some uncertainty exists as to the actual biomass values during the years under consideration (Cram, in press). However, for the present calculations, only relative stock sizes are required. Two sets of biomass data were used (Table II):

Biomass I – Newman (1970) estimated biomass to be approximately 5,7 million metric tons from 1957 to 1960 and 6,8 million metric tons from 1963 to 1966. As an estimate was not made for 1961 and 1962, a value of 6,8 million metric tons is assumed. In order to obtain biomasses for 1967 to 1971, the relationship between the 1966 catch per unit effort (c.p.u.e.) of Schülein *et al.* (1975) and the 1966 biomass as estimated by Newman (*op. cit.*) was used to raise the actual c.p.u.e. for these years.

Biomass II – biomass estimates calculated from Virtual Population Analysis are also used (Schülein *et al.* 1975). V.P.A. uses the number of fish landed per age group to obtain biomass values, and is therefore partially dependent upon age readings which may be subject to considerable error and, thus, more confidence is placed in the former set of stock sizes, the results of which are given in more detail. However, because the two sets of data show different trends over the early part of the tagging programme, both are summarized.

RESULTS

The number of tags returned per cohort per year (n_t), N_t and Z′ are presented in Table III.

Table II: Fleet hold capacity and pilchard catch, c.p.u.e. and biomass

Year	Pilchard catch (× 10^3 metric tons)		Fleet hold capacity (metric tons)	C.p.u.e. (metric tons landed per litre fuel)	Biomass (× 10^6 metric tons)	
	Land-based	Total			I*	II†
1958	228	228	3 028	—	5,7	3,0
1959	271	271	2 990	—	5,7	3,0
1960	284	284	2 822	—	5,7	3,0
1961	340	340	3 204	—	6,8	3,2
1962	395	395	3 554	—	6,8	3,4
1963	555	555	3 795	—	6,8	3,8
1964	621	621	5 610	—	6,8	4,2
1965	666	666	5 683	0,103	6,8	4,7
1966	668	718	6 179	0,107	6,8	5,4
1967	706	932	6 018	0,080	5,2	6,2
1968	807	1 387	7 320	0,068	4,4	5,2
1969	630	1 111	9 263	0,049	3,2	3,6
1970	514	514	9 265	0,040	2,6	2,7
1971	269	325	10 247	0,024	1,5	3,3

* Estimated from Newman (1970) and c.p.u.e. data
† Estimated from V.P.A. (Schülein *et al.* 1975)

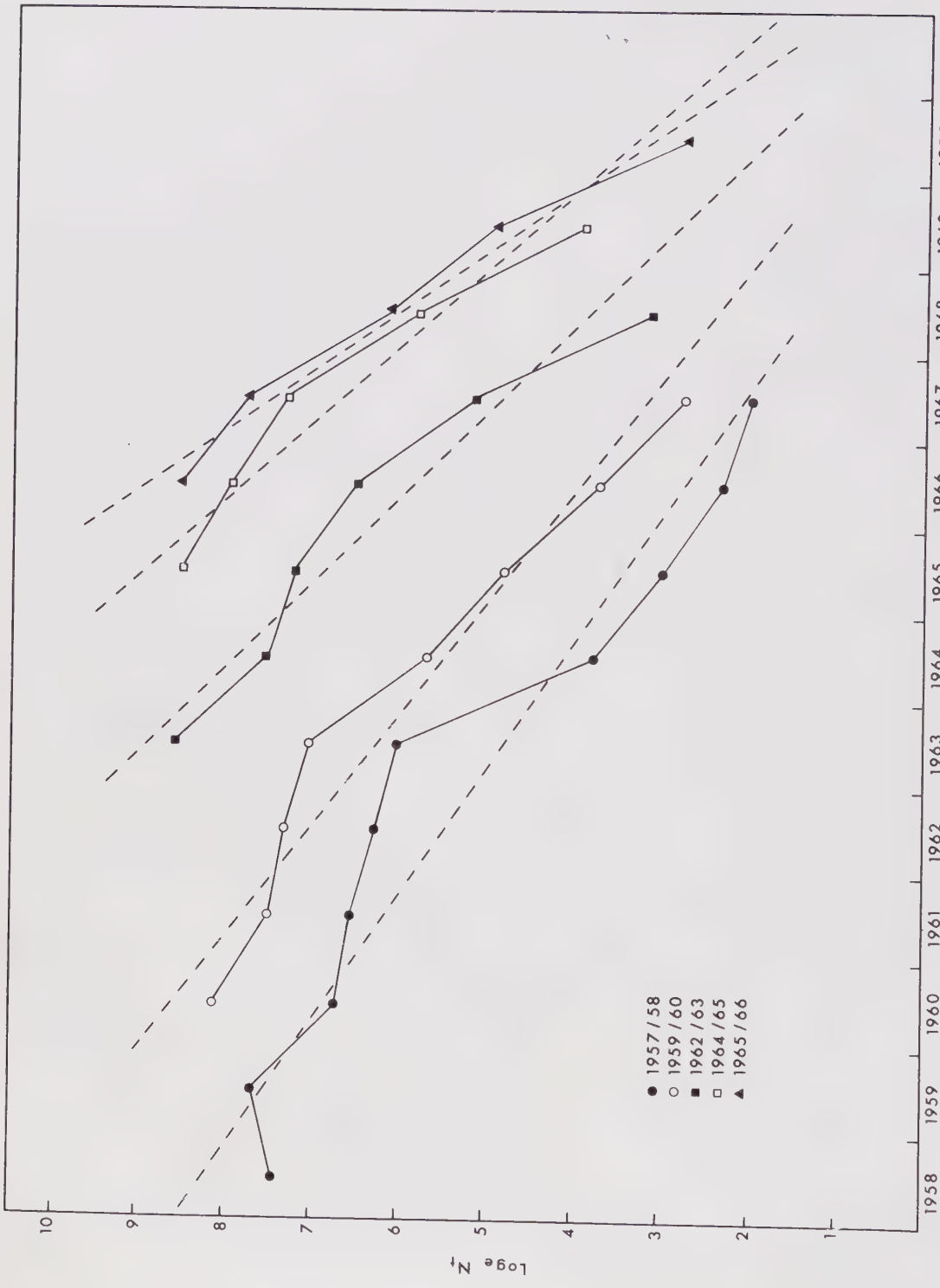

Fig. 1: Log_e N_t values per year per cohort (solid) and least squares regression lines (broken)

Table III: Tags returned (n_t), calculated number of tags in the stock (N_t) and Z′ values per year per cohort for biomass I and mean Z′ values and regression coefficients for both sets of biomass

Year	1957/58			1959/60			1962/63			1964/65			1965/66			Biomass I	Biomass II
	n_t	N_t	Z′	n_t	N_t	Z′	n_t	N_t	Z′	n_t	N_t	Z′	n_t	N_t	Z′	$\overline{Z}'$	$\overline{Z}'$
1958	67	1 666															
			+0,21													+0,21	+0,21
1959	99	2 071															
			−0,93													−0,93	−0,93
1960	41	818		171	3 414												
			−0,15			−0,63										−0,39	−0,51
1961	35	700		91	1 821												
			−0,27			−0,23										−0,25	−0,19
1962	31	534		84	1 447												
			−0,25			−0,22										−0,24	−0,13
1963	34	416		94	1 152		434	5 321									
			−2,26			−1,36			−1,04							−1,20	−1,10
1964	4	44		27	296		172	1 884									
			−0,72			−0,88			−0,32							−0,60	−0,48
1965	2	20		12	122		134	1 369		491	5 016						
			−0,70			−1,10			−0,71			−0,57				−0,64	−0,52
1966	1	10		4	41		66	672		280	2 852		503	5 123			
			−0,32			−0,98			−1,38			−0,63			−0,78	−0,93	−1,03
1967	1	7		2	15		22	161		207	1 516		321	2 351			
									−2,04			−1,51			−1,66	−1,59	−1,65
1968	0			0			4	22		61	336		81	446			
												−1,89			−1,19	−1,54	−1,58
1969	0			0			0			10	51		27	136			
															−2,18		
1970	0			0			0			0			3	15			
1971	0			0			0			0			0				
Regression coefficients:																	
Biomass I			−0,69			−0,78			−1,00			−1,12			−1,43		
Biomass II			−0,61			−0,73			−0,85			−1,00			−1,40		

Biomass I (Table II) was used to calculate N_t, the values for which are plotted in natural logarithms in Figure 1. Z′ values averaged from several cohorts were calculated for each year and, together with the regression coefficients for each cohort, are shown in Table III. For the average Z′ values and the regression coefficients, two sets of results corresponding to the two sets of biomass in Table II are given to enable comparison to be made.

DISCUSSION

Both Table III and Figure 1 show that Z′ has increased considerably over the period studied. The reason for the positive values of Z′ for 1958/59 is not known but a possible explanation would be an incomplete reporting of tags in 1958 as mentioned by Newman (1970). The use of both sets of biomass values only alters the degree of increase and not the overall trend. Closer analysis suggests that an abrupt increase in Z′ occurred in 1963/64. In 1963, owing to higher quotas, the catch increased by 41 per cent and it is thus probable that an increase in fishing mortality (F) may have been responsible for this increase in Z′. From 1965 onwards, Z′ started to increase rapidly (Table III and Figure 1). Table II clearly shows the increase in exploitation rates associated with this increase in Z′. The total pilchard catch from 1958 to 1968 increased by 508 per cent but subsequently decreased towards its initial figure. C.p.u.e. decreased steadily by 329 per cent from 1965 to 1971 whereas fleet hold capacity progressively rose from 3 028 metric tons in 1958 to 10 247 metric tons in 1971, an increase of 238 per cent.

The number of tags in the available commercial stocks is also affected by the emigration of tagged fish (equation 2, E). Newman (1970) considered that the increase in fishing area between the period 1957–1960 and the period 1963–1966 reduced the number of fish that could stray beyond the fishery and that this had been responsible for the 20 per cent decrease in his coefficient of emigration and natural mortality. No factor is introduced in the present report to correct for this decrease. If incorporated, it would effectively steepen the decay rates for the 1964/65 and 1965/66 cohorts still further.

Losses due to sustained tagging mortality (M′) and other losses (U) as discussed previously have probably remained constant, because the methods of tagging and collection have remained the same.

Natural mortality (M) is another component of Z′ for which very little information exists. It is possible that when pilchard stock size declined, the decrease in predator stock size lagged behind, causing a proportional increase in predation pressure. R. J. M. Crawford (Sea Fisheries Branch, personal communication) found that a decrease in magnitude of the pelagic stocks of the Western Cape was followed by a substantial decrease in the sea bird population, owing to a reduction in breeding. It is possible that seal and snoek populations would be similarly affected.

From the evaluation of the factors considered in equation 2, it appears that the most significant contributor to the increase in Z′ has been a rise in fishing mortality. In 1967, tags were being recovered from the 1957/58 and 1959/60 cohorts which had been in the sea for 9 and 10 years (Fig. 1). However, by 1970 no tags were being recovered later than 5 years after the date of tagging. It can be concluded that the maximum age of fish in the catch was reduced considerably between 1958 and 1971, largely as a result of the impact of fishing mortality on the population structure.

ACKNOWLEDGEMENTS

The authors thank Dr D. S. Butterworth, Dr D. L. Cram and Mr R. J. M. Crawford for their helpful suggestions during the preparation of the manuscript.

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Fish. Bull. S. Afr. 10:15–19
1978

AN ANALYSIS OF THE VARIABILITY IN BONGO NET CATCHES OF PILCHARD EGGS OFF SOUTH WEST AFRICA

D. P. F. KING and A. A. ROBERTSON

Since 1971 fish egg and larva research has formed an important part of the South West African pelagic research programme of the Sea Fisheries Branch. The research was primarily orientated towards the pilchard *Sardinops ocellata* Pappe, the main objective being to estimate the abundance of the adult pilchard population on the basis of spawning production.

Two questions arise when fish egg populations are sampled to estimate their abundance. Firstly, does the sample accurately represent the column of water filtered and secondly, is the sample from a single station representative of a larger area? Thus, an assessment of sampling variability is necessary in order to judge realistically the reliability of the estimates.

In this study, observations on variability were based on two series of replicate oblique tows of a paired, modified, Brown-McGowan Bongo net sampler (Posgay *et al.* 1968). This net, which is widely accepted as the most efficient sampler available for the quantitative sampling of ichthyoplankton (Ahlstrom *et al.* 1973), had a mouth diameter of 0,57 m, a cylindrical section 1,35 m long and a tapered conical section 2,5 m long. Nylon monofilament netting with mesh sizes of 500 µm (left unit) and 940 µm (right unit) was used throughout.

The samples were collected off the coast of South West Africa by the R. S. *Benguela* (Fig. 1). The sampling location (21°–23°20′S) is in an area of known pilchard spawning (King 1977). The first series, made in January 1975, was designed to assess the haul-to-haul variability within a sampling area and consisted of 19 tows taken at random in a 5 x 5 nautical mile area in the vicinity of 22°40′S, 14°07′E. A 25 square mile area was selected as it approximated the area represented by an inshore station in the South West African Pelagic Egg and Larva Survey (SWAPELS) sampling grid (King and Robertson 1973). The second series, made in March 1975, was designed to give a measure of the haul-to-haul variation in replicate oblique tows at a single station. On this occasion, the net was hauled 15 times over the same path. To facilitate replication, the direction of the ship was reversed after each haul in an attempt to sample

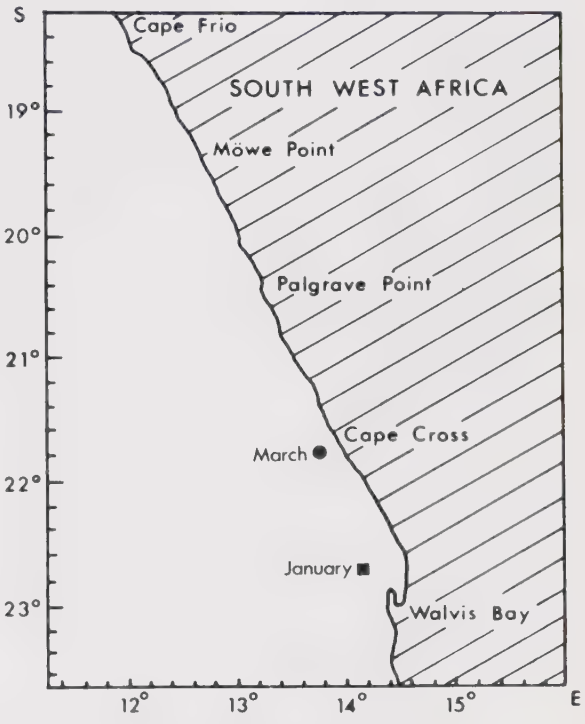

Fig. 1: Sampling locations

the same parcel of water.

During both series, each tow was made in an even oblique manner to a depth of 50 m so as to encompass the vertical distribution of the eggs. A time-depth recorder gave a record of tow characteristics and the volume of water filtered was determined from a digital flow-meter in the mouth of the net. A ship's speed of 2 knots was maintained as evenly as possible throughout each tow. Sampling conditions (sea state, equipment performance) during both series of hauls were almost ideal. Details of the tows made during both series are given in Table I.

The laboratory treatment of the material from both series of tows was identical. All the pilchard eggs were removed from each sample and

Table I: Sampling details of replicate series of tows

Haul number	Series I January 1975					Series II March 1975				
	Time	Volume filtered (m^3)		Speed (m/sec)	Depth (m)	Time	Volume filtered (m^3)		Speed (m/sec)	Depth (m)
		Left unit	Right unit				Left unit	Right unit		
1	09h46	113	121	1,36	43	11h15	126	126	1,66	24
2	10h10	109	104	1,20	56	11h36	129	140	1,54	30
3	10h27	128	118	1,52	40	12h01	180	185	1,70	40
4	10h45	120	113	1,46	37	12h20	191	204	1,68	40
5	11h21	96	90	1,05	59	12h45	187	204	1,80	30
6	11h37	103	96	1,27	45	13h01	219	248	1,92	28
7	12h18	101	95	1,30	46	13h35	136	154	1,23	50
8	12h33	105	97	1,30	51	14h00	146	157	1,02	64
9	12h48	115	109	1,39	43	14h16	92	102	1,10	55
10	13h00	122	117	1,39	49	14h30	132	146	1,60	30
11	13h19	127	120	1,57	41	14h48	122	127	1,40	38
12	13h31	135	128	1,49	37	14h59	98	107	1,14	50
13	13h43	119	112	1,40	44	15h10	114	116	1,26	38
14	13h56	126	118	1,37	40	15h30	175	180	1,22	37
15	14h12	111	105	1,21	51	15h42	98	107	1,40	34
16	14h31	97	91	1,24	58	—	—	—	—	—
17	14h49	103	96	1,20	48	—	—	—	—	—
18	15h05	114	107	1,42	37	—	—	—	—	—
19	15h17	107	120	1,45	38	—	—	—	—	—

counted, and the variability resulting from differences in volumes was eliminated by standardizing to the number under 10 square metres of sea surface. The method of adjustment of the data to a standardized count was that employed for the Pacific sardine by Kramer *et al.* (1972).

WITHIN-TOW VARIABILITY

The number of eggs found in each haul of both series is shown in Table II. An examination of the distribution of egg counts for both series shows a characteristically large number of tows with zero counts in conjunction with high counts (Table II). A probable explanation for such large variation between certain net pairs is that the sampler bordered on the periphery of pilchard egg patches, which, it would seem, are sharply delineated. The mean number of eggs in an area would be significantly influenced by the presence of a few zero counts. Thus, it seems reasonable to conclude that if the catches from the left and right units of a sampler could be considered related, a gain in accuracy would be achieved by pooling within-tow observations. With this in mind, an investigation of the data was conducted to assess the similarity of paired observations, i.e. to determine whether there was a significant association between catches of the left and the right units of the Bongo net sampler.

An appropriate statistical procedure for an analysis of this type is a non-parametric, distribution-free, signed-rank test; Wilcoxon's test is the most widely used. Results of this test showed no significant difference between net pairs for either series of data ($P<0,05$). Observations were therefore combined giving one value for each haul. The combined value for the hauls in series I and II are given in Table III.

VARIANCE ASSOCIATED WITH A SINGLE STATION

The combined data comprising series II was not normally distributed, and an effort was therefore made to counteract the skewness of the distribution. The counts were initially log-transformed to normalize the data, thus facilitating subsequent statistical analysis.

The coefficient of variation (V_x), calculated

Table II: Number of pilchard eggs taken by the replicate hauls in both series of tows

Haul number	Series I January 1975				Series II March 1975			
	Actual number		Standardized number		Actual number		Standardized number	
	Left unit	Right unit	Left unit	Right unit	Left unit	Right unit	Left unit	Right unit
1	75	40	285	142	40	49	76	93
2	0	64	0	345	92	94	214	201
3	259	7	809	24	158	187	351	404
4	30	191	92	625	77	99	161	194
5	0	41	0	269	71	173	114	254
6	345	0	1 507	0	162	184	207	208
7	37	205	168	993	63	34	232	110
8	34	20	165	105	75	0	329	0
9	382	105	1 428	414	27	30	161	162
10	336	0	1 350	0	150	157	341	323
11	134	821	433	2 805	67	21	209	63
12	37	460	101	1 330	63	44	321	206
13	30	112	111	440	41	44	137	144
14	204	55	648	186	81	84	171	173
15	67	0	308	0	0	87	0	276
16	19	48	114	306	—	—	—	—
17	27	68	126	340	—	—	—	—
18	170	49	552	169	—	—	—	—
19	144	30	511	95	—	—	—	—

using the log-transformed data, was used as a measure of variability. Bagenal (1955) showed that the relationship between the variance of a log-normal variable and the coefficient of variation of the original variable is

$$\sigma_y^2 = 0{,}43428 \log_{10}(1 + V_x^2)$$

where σ_y^2 is the variance of the log-normal variable and V_x^2 is the relative variance of x. The calculated variance (σ_H^2) of the log-transformed data is 0,0256. Thus, using the above expression, the coefficient of variation for the 15 replicates is given as

$$V_x = \left[\text{antilog}_{10}\left(\frac{0{,}0256}{0{,}43428}\right) - 1\right]^{\frac{1}{2}}$$

Solution of this equation gives $V_x = 0{,}3808$, i.e. a variation of 38 per cent can be expected between replicate tows. Also, the 95 per cent confidence limits associated with the mean of the hauls are of interest. These were calculated as 81–122 per cent.

In estimating confidence limits of a series of hauls, Bagenal (1955) showed that once the data have been log-transformed, transforming the results back does not give the original data. The mean of the transformed data gives, as its antilogarithm, the geometric mean of the original data and not the arithmetic mean. Thus, all confidence limits calculated from the mean of the transformed data refer to the geometric mean and should be compared in the transformed state.

Table III: Combined numbers of pilchard eggs taken by the replicate hauls in both series of tows

Haul number	Series I January 1975		Series II March 1975	
	Actual number	Standardized number	Actual number	Standardized number
1	115	212	89	85
2	64	168	186	207
3	266	435	345	378
4	221	350	179	178
5	41	130	244	187
6	345	780	346	207
7	242	568	97	167
8	54	137	28	158
9	487	935	57	162
10	336	689	307	331
11	955	1 585	88	134
12	497	699	107	261
13	142	270	85	140
14	259	425	165	172
15	67	158	87	144
16	67	206		
17	95	229		
18	219	367		
19	174	291		

VARIANCE ASSOCIATED WITH A STANDARD AREA

As was the case with series II, the observations from series I were not normally distributed and were therefore log-transformed prior to analysis.

The total variance (σ_H^2) associated with the hauls taken in series I (Table III) was calculated as 0,0943. Thus, the coefficient of variation (V_x) is calculated from the equation:

$$\sigma_H^2 = 0{,}0943 = 0{,}43428 \log_{10} (1 + V_x^2),$$

yielding the solution: $V_x = 0{,}8056$. Thus, a variation of 81 per cent is associated with the mean of the hauls taken in a 25 square nautical mile area. The 95 per cent confidence limits around the mean of the transformed data, and thus the limits around the geometric mean of the untransformed data, were calculated as 71–141 per cent.

DISCUSSION

Silliman (1946) investigated the variability of egg numbers of the Pacific sardine *Sardinops caerulea* in oblique tows and concluded that a single egg count may be considered as statistically significantly different from another if it is less than one half or more than double the other. The results of the present study compare favourably with those of Silliman (*op.cit.*) for a single station, but are considerably lower in the case of the variability associated with a standard sampling area. However, this would be expected, as an analysis of the variability of pilchard eggs within a standard sampling area shows a variation considerably greater than the variation observed in the analysis of a single station. It appears that these findings justify the basic assumption of quantitative sampling, i.e. that the sample taken is representative of the volume of water filtered. However, it is evident that the error associated with this assumption is relatively small in comparison with that introduced by integrating samples over space. Thus, it is suggested that the variability within a specified area is a more realistic base from which to assess the accuracy of pilchard egg estimates.

Non-random spatial distribution is a recognized feature of plankton. Pilchard egg populations are no exception and exhibit a high degree of over-dispersion (Taft 1960). This is confirmed in the present study. As both series of hauls were taken under near ideal conditions, sampling variation could not be attributed entirely to technical error (e.g. variation in haul velocity). It is more feasibly explained by a non-random distribution of the eggs. It is probable, therefore, that patchiness is the most important element of sampling error. This error can be partly reduced by increasing the volume of water filtered and thereby obtaining a larger sample. Wiebe (1971), in his study on zooplankton patchiness, postulated that lengthening the tow results in a significant improvement in precision, not directly related to increasing the volume of water filtered but apparently to the increase in the probability of sampling the "right" number of patches. Our evidence has indicated that, within a relatively small area, pilchard eggs are sharply delineated into patches. Thus, it is reasonable to suggest that Wiebe's (*op. cit.*) sampling criteria should be adopted and that in order to increase the accuracy and precision in the estimation of pilchard egg abundance, one should increase the volume of water filtered through longer tows rather than by increasing the size of the sampler used.

ACKNOWLEDGEMENTS

The authors wish to thank the captain and crew of the R. S. *Benguela* for their assistance during the cruises and Mr C. J. Giddey who meticulously sorted and counted the pilchard eggs.

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ASPECTS OF THE EARLY LIFE HISTORY OF THE HAKE *MERLUCCIUS CAPENSIS* CASTELNAU OFF SOUTH WEST AFRICA

M. J. O'TOOLE

Hake of the genus *Merluccius* occur off the south and west coasts of southern Africa at depths of 40–1 000 m (Smith 1965). Commercially, they are the most important trawl-caught fish taken in these waters.

Catches of hake off southern Africa have increased tenfold in only 10 years, from 106 700 metric tons in 1962 to over a million tons in 1972 (Draganik 1974). In recent years, there has been a rapid expansion in fishing effort for this species particularly off South West Africa by distant-water fleets of several countries, and landings have correspondingly increased from 86 800 metric tons in 1968 to 568 000 metric tons in 1972 (Ikeda 1975). The stocks are exploited mainly by vessels of Bulgaria, Cuba, South Africa, Soviet Union and Spain. Soviet vessels alone take more than 75 per cent of the total hake catch from these waters (F.A.O. 1974).

Two species of hake are recognized off the coast of southern Africa, namely *Merluccius capensis* Castelnau, and *M. paradoxus* Franca. The distinction between the two forms is based chiefly on differences in the number of vertebrae, otolith structure and gill-raker pigmentation (Van Eck 1969, Botha 1971). The species also differ in depth distribution, *M. capensis* tending to be found inshore, whereas *M. paradoxus* prefers the deeper water off shore (Botha *op. cit.*, Kuderskij 1973 quoted from Porębski 1976). Owing to the difficulty in visually distinguishing between the two species, catches are usually referred to simply as *Merluccius* spp.

Chłapowski (1975) reported that the quantitative occurrence of the two species showed differences from north to south. Catches off South West Africa were almost exclusively *M. capensis*, but the catch frequency of *M. paradoxus* increased southwards towards the Cape grounds where the species eventually became dominant. Both species spawn throughout the year (Jones and Van Eck 1967), *M. paradoxus* at greater depths than *M. capensis* (Pschienichniy and Assorov 1969 quoted from Porębski 1976, Botha 1973). However, the main spawning season generally extends from September to December.

Hake generally exhibit marked diurnal vertical movement, but during the spawning season shoals become more pelagic than at other times of the year and show little diurnal movement (Botha 1973). A similar phenomenon was reported by Dark (1975) for the Pacific hake *M. productus*. Spawning in the Cape hakes apparently takes place at intermediate depths during the pelagic phase (Botha *op. cit.*).

Despite the commercial importance of the hake around southern Africa, there is little information on the distribution, seasonal abundance or ecology of the planktonic eggs and larvae in these waters. Previous work on the early life history of the hake has been concerned mainly with descriptions of the egg and the larva (Matthews and De Jager 1951, Haigh 1972). Hake larvae were reported in the plankton off South West Africa by Hart and Marshall (1951). The only other reference is a general account of the occurrence of eggs and larvae between the Cunene River (17°S) and the Agulhas Bank (37°S), based on a two-month investigation by Porebski and Koronkiewicz (1975).

During the period 1972–1974, the Sea Fisheries Branch conducted an extensive ichthyoplankton programme off South West Africa (SWAPELS) with the aim of investigating the early life history of the commercially important pelagic species, i.e. the pilchard *Sardinops ocellata* Pappe and the anchovy *Engraulis capensis* Gilchrist. The stations shown in Figure 1 were occupied monthly between August 1972 and March 1973 (survey 1) and between August 1973 and March/April 1974 (survey 2).

At each station, oblique hauls were made in the 0–50 m layer (depth permitting) using paired Bongo nets 57 cm in diameter with meshes of 0,940 mm (survey 1) and 0,500 mm and 0,940 mm (survey 2). A detailed account of the method of collection is given by King and Robertson (1973) and O'Toole (1977b). Station positions and depths are documented by O'Toole (1976). In order to allow for variation in volume of water strained as a result of fluctuations in speed and different duration of tows, the method of Kramer *et al.* (1972) was used to standardize to the number of larvae under 10 m^2 of sea surface. However, no attempt was made to correct for different surface areas represented

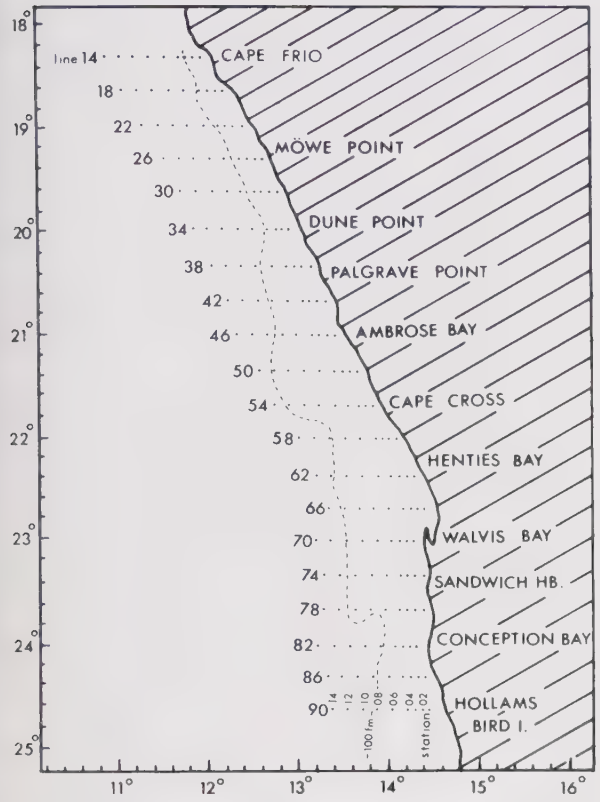

Fig. 1: Location of routine stations occupied during the SWAPELS cruises in 1972/73 and 1973/74

by the stations in the grid or for cases where no larvae were caught. All subsequent deductions and statements are based on the standardized totals unless mentioned otherwise.

Hake eggs and larvae were common in the plankton samples, the larvae ranking seventh in order of species abundance.

A brief description of the egg and egg distribution is given here and the seasonal distribution and relative abundance of larvae are described. Hydrological affinities, dispersal and diurnal variation in catches of larvae are also discussed.

RESULTS

Identification of eggs and larvae

Hake eggs collected during this study were identified from descriptions given by Matthews and De Jager (1951), aided by descriptive literature on the early life history of hake species from other parts of the world (d'Ancona 1933, Ahlstrom and Counts 1955, Arbault and Boutin 1968, De Ciechomski and Weiss 1973). The larvae were easily recognized from the illustration given by Hart and Marshall (1951) and the more comprehensive description of *M. capensis* larvae by Haigh (1972).

The eggs are spherical with a smooth (unsculptured) membrane, a narrow perivitelline space and a single oil globule. The diameter of the eggs ranged from 0,85 mm to 1,06 mm (mean 0,94 mm) and that of the oil globule from 0,15 mm to 0,26 mm (mean 0,22 mm). The ranges within size categories of 200 eggs extracted from random samples are shown in Table I. Approximately 80 per cent of those measured were between 0,90 mm and 1,00 mm in diameter, closely agreeing with the size range of eggs recorded by Matthews and De Jager (1951) and Porębski and Koronkiewicz (1975).

Owing to the difficulty in separating the two adult hake species, even greater difficulty was anticipated in distinguishing between species at the egg and larval stages. During the routine cruises, eggs of both species might have been collected in the samples, but no attempt was made to separate them. Larval and juvenile hake were indistinguishable from those described as *M. capensis* by Haigh (1972).

Porębski and Koronkiewicz (1975) reported that hake eggs taken in the plankton north of the Orange River were slightly smaller than those found further south and they also noted certain differences in larval pigmentation, though these were not specified. In view of the latitudinal variation in egg size and the corresponding regional distribution of the two species (Chłapowski 1975), it is probable that the eggs and larvae collected in this investigation were predominantly those of *M. capensis*.

Table I: Diameter of 200 hake eggs according to size categories

Number of eggs	Egg diameter (mm)	Oil globule diameter (mm)
32	0,81–0,90	0,15–0,21
84	0,91–0,95	0,18–0,24
76	0,96–1,00	0,17–0,24
8	1,01–1,10	0,20–0,26

Distribution of eggs

Hake eggs were identified in the samples but were not counted. However, the limited observations on egg distribution showed that the southern part of the research area was the main centre of spawning. Eggs were found between October and December during survey 1 and from September to January on survey 2, noticeably more eggs being taken in the vicinity of Walvis Bay, particularly during November and December. Eggs and newly hatched larvae frequently occurred in the same haul.

The findings in general substantiate those of other workers. Chłapowski (1974) found that the gonads of *M. capensis* caught between latitudes 15°S and 20°S were immature during November, but during the same month, over 60 per cent caught between 20°S and 25°S were maturing, spawning or spent. Porębski and Koronkiewicz (1975) also noted large numbers of eggs and larvae off Walvis Bay in November/December.

Distribution and seasonal abundance of larvae

Although hake larvae were found over the entire research area during both surveys, more than 94 per cent of the specimens were taken from waters south of Palgrave Point. Abundance declined sharply further north, 3,9 per cent being recorded in 1972/73 and 5,1 per cent in 1973/74. The percentage collected in each part of the survey area during the two years is summarized in Table II.

Larvae were captured over the entire range of the sampling grid from inshore to off shore but were most numerous 50–100 km from the coast (Table III). The geographical distribution to the north and west was adequately encompassed but that to the south was not. The general distribution and the main centre of abundance were very similar for both surveys (Figs. 2 and 3). Highest densities were noted 40–60 km north-west of

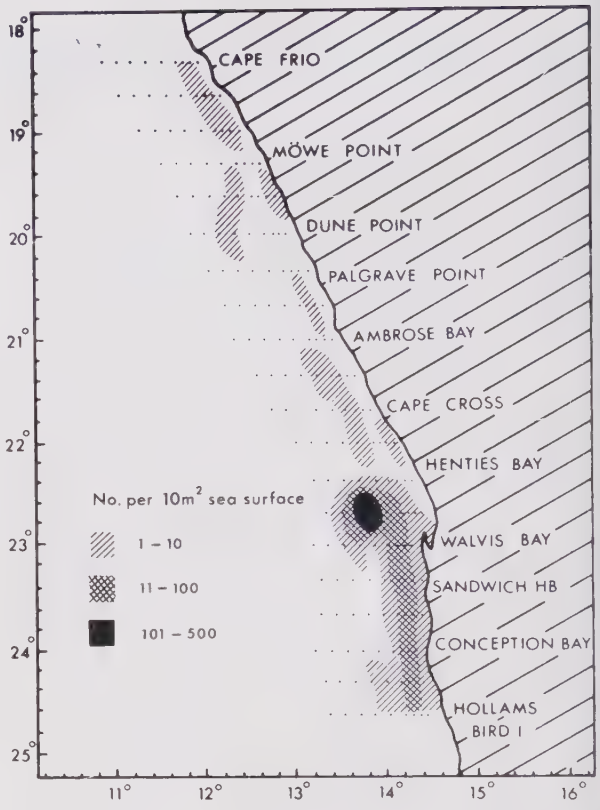

Fig. 2: Distribution and abundance of hake larvae during survey 1 (values represent cumulative standard haul totals for all cruises)

Table II: Percentage of hake larvae taken in each part of the survey area

Area	Station line	Survey 1	Survey 2
Cape Frio – Möwe Point	14–26	1,9	2,9
Möwe Point – Palgrave Point	30–42	2,0	2,2
Palgrave Point – Henties Bay	46–58	1,7	8,8
Henties Bay – Sandwich Harbour	62–74	67,4	70,6
Sandwich Harbour – Hollams Bird Island	78–90	27,0	15,5

Walvis Bay. Hake larvae, nevertheless, were 31 per cent more plentiful (standardized positive hauls) in 1973/74 than in 1972/73, December 1973 being overall the most productive month.

Although sampling was conducted from August to March/April, larvae were only encountered from October in each survey. Ninety-two per cent of the total captured (both surveys combined) were taken in October, November

Table III: Percentage occurrence of hake larvae in relation to distance from the shore

Distance from shore	Survey 1	Survey 2
± 8–10 km	1,2	3,2
10–20 km	12,3	5,0
20–30 km	22,3	9,0
30–50 km	22,3	9,9
50–100 km	41,5	72,2
100 km or more	0,3	0,5

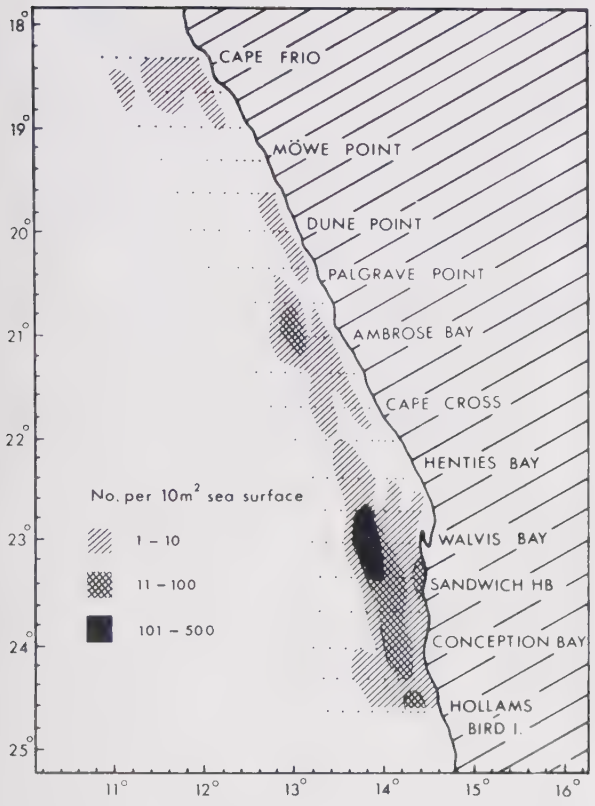

Fig. 3: Distribution and abundance of hake larvae during survey 2 (values represent cumulative standard haul totals for all cruises)

and December. Over 60 per cent were caught during December. Specimens found between January and March/April accounted for only 8 per cent of the total.

Survey 1 (August 1972 to March 1973) – The monthly distribution and relative abundance of hake larvae, together with surface isotherms, are shown in Figure 4 and the monthly length composition in Figure 5. A summary of the monthly hauls and abundance is given in Table IV. All localities mentioned in subsequent discussion are shown in Figure 1.

Hake larvae first occurred in the plankton during October near Walvis Bay when 10 specimens ranging from 6 mm to 14 mm long were captured. The time taken for hake to complete larval development is unknown. However, Ahlstrom and Counts (1955) estimated that it takes at least a month, depending upon the temperature of the water. It is therefore probable that larvae taken during October resulted from eggs spawned some time in September.

More larvae were caught in November, mainly inshore south of Cape Cross. The centre of abundance was 20–30 km west of Walvis Bay, but a few isolated specimens were found off shore north of Cape Cross. Most of the larvae (80 per cent) consisted of yolk-sac and other early stages hatched from eggs spawned during October and early November.

Largest numbers were taken during December, predominantly south of Cape Cross, 8–100 km from the coast. Hake larvae were particularly common 80–100 km north-west of Walvis Bay. More than 60 per cent of the specimens captured in December were longer than 12 mm and probably originated from heavy spawning in November. It is also possible that some of the November larval cohorts were represented in the December catches.

A sharp drop in abundance was noticeable in January. Only a few isolated specimens were captured at scattered localities between Möwe Point and Walvis Bay. They measured from 5 mm to 12 mm, which suggested that some localized spawning had taken place in December.

Table IV: Summary of the monthly hauls and abundance of hake larvae during survey 1

Cruise dates	Total number of hauls	Number of positive hauls	Number of larvae collected		Mean number collected per standardized positive haul	Percentage of standardized total number collected
			Actual	Standardized		
August 22–31	126	0	—	—	—	—
September 15–20	126	0	—	—	—	—
October 15–22	156	2	10	11,0	5,5	1,6
November 11–19	180	21	123	132,3	6,3	19,3
December 5–14	180	20	512	510,0	25,5	74,3
January 13–21	180	6	19	19,8	3,3	2,9
February 14–24	177	0	—	—	—	—
March 11–19	177	3	9	13,5	4,5	2,0

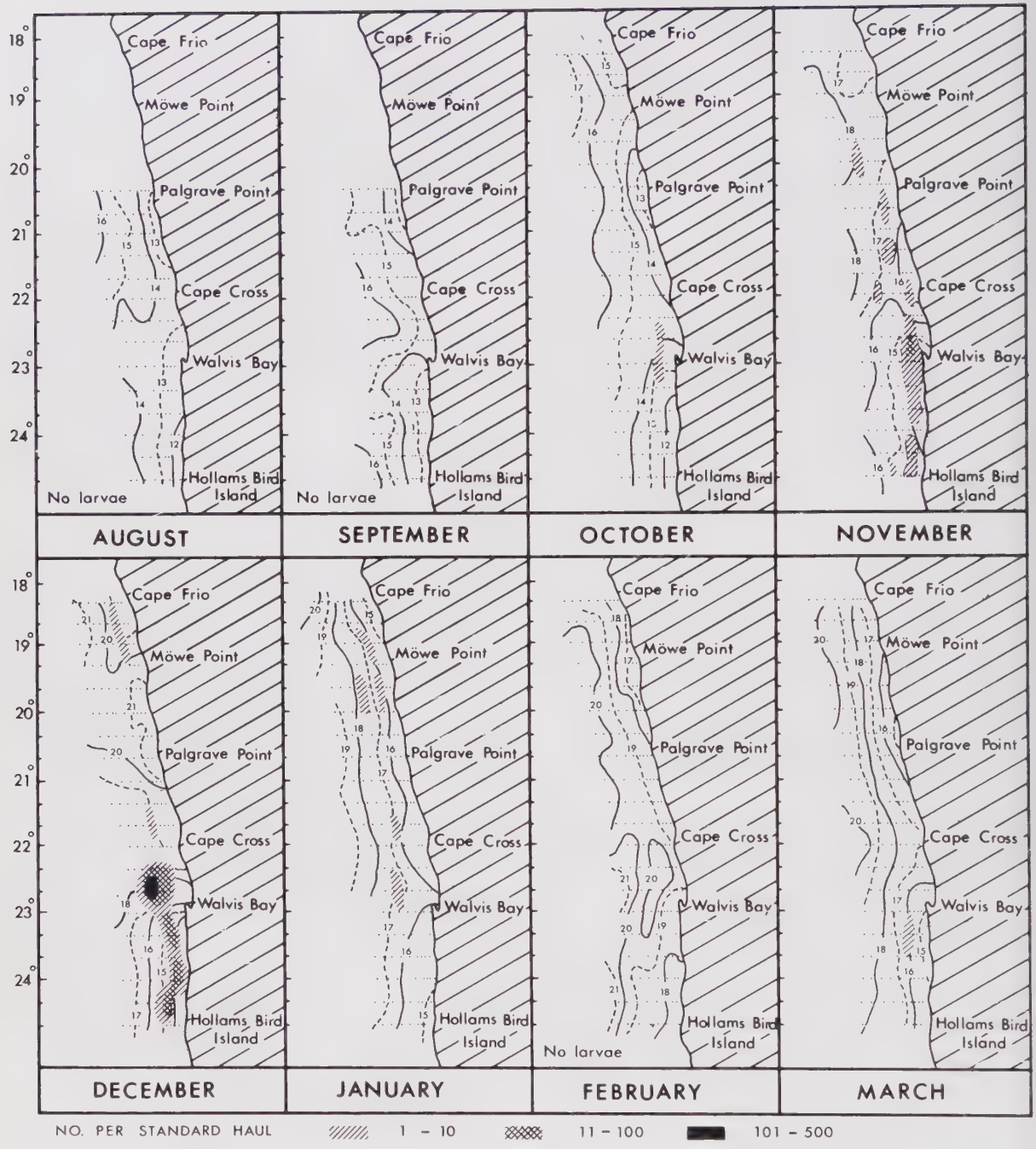

Fig. 4: Monthly distribution and abundance of hake larvae, August 1972 to March 1973

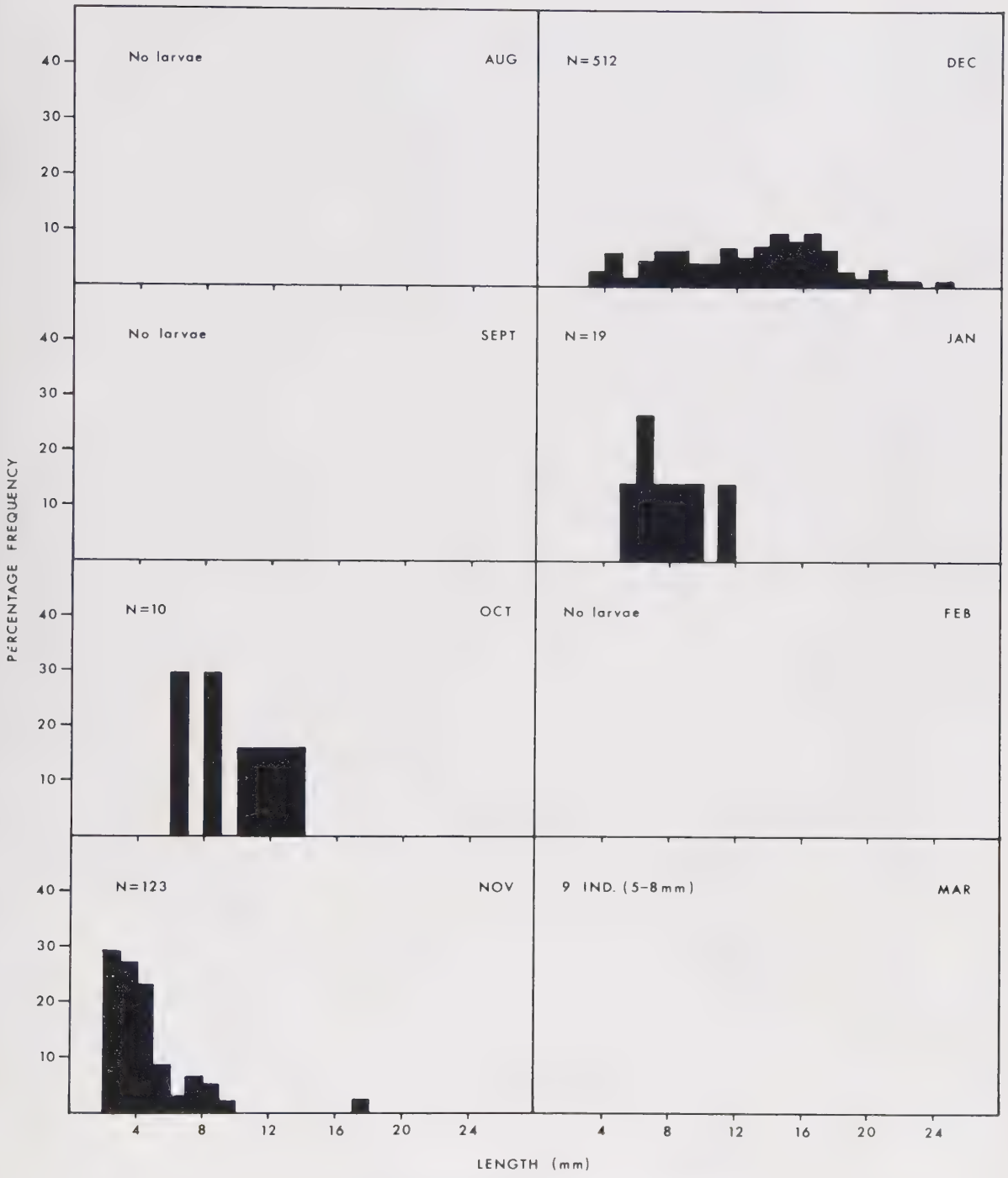

Fig. 5: Length composition of hake larvae collected during the survey cruises August 1972 to March 1973

No larvae were taken in February. Only nine specimens were found in March, 20–50 km from the coast south of Walvis Bay. These larvae were 5–8 mm in length and were presumably derived from eggs spawned during late February and early March.

Survey 2 (August 1973 to March/April 1974) – The monthly distribution and relative abundance of hake larvae, together with surface isotherms, are illustrated in Figure 6. A summary of the hauls and larval abundance is given in Table V and the monthly length frequencies in Figure 7.

Larvae were initially collected in the plankton in October at isolated localities between Möwe Point and Conception Bay but mainly inshore south of Walvis Bay. The specimens caught were 4–15 mm long but predominantly less than 8 mm.

The distribution in November was similar to that of October but the number caught increased considerably. Largest catches were made in the south, 30–60 km off shore between Walvis Bay and Conception Bay. Larvae were also common further south at inshore stations near Hollams Bird Island. The length distribution showed that over 80 per cent of those captured were newly hatched. An intensification of spawning must therefore have occurred during late October and early November. The remainder of the larvae were between 14 mm and 25 mm in length and probably represented the same cohort as was sampled during October.

The December cruise produced the largest catch of hake larvae in survey 2. Concentrations were found south-west of Palgrave Point and in the vicinity of Walvis Bay. The centre of greatest abundance was 40–64 km west of Walvis Bay at a similar location to that of the November cruise. Over 90 per cent of the specimens were newly hatched (3–8 mm long), indicating heavy spawning during late November and early December.

By January, larvae had become scarce in the plankton. A few isolated patches of specimens with lengths ranging from 4 mm to 20 mm were found off shore north-west of Walvis Bay.

In February, the number of larvae declined even further. A few recently hatched specimens were found south-west of Cape Frio, west of Palgrave Point and south-west of Walvis Bay.

Hake larvae were slightly more common during March/April, the regional distribution being similar to that of February. Many of the specimens were newly hatched, which suggested that sporadic spawning was still occurring at isolated localities in March.

Diurnal variation in catches of larvae

A comparison of the total, unstandardized number of hake larvae for both surveys taken in all positive hauls at different times showed that larvae were equally abundant during the day and the night (Table VI and Fig. 8). Nevertheless, diurnal differences existed when larval size was considered.

Newly hatched larvae (those less than 5 mm in length) were caught mainly between 02h00 and 14h00. Maximum catches were made in hauls taken between 12h00 and 14h00.

In contrast, the older larvae (those longer than 10 mm) were practically absent from daylight collections, the percentage occurrence increasing markedly after dusk and reaching a peak between midnight and 02h00. Towards early morning, numbers dropped sharply and few were caught after 08h00. Larvae of intermediate sizes (5–10 mm) were common in both day and night hauls but were about twice as abundant in

Table V: Summary of the monthly hauls and abundance of hake larvae during survey 2

Cruise dates	Total number of hauls	Number of positive hauls	Number of larvae collected		Mean number collected per standardized positive haul	Percentage of standardized total number collected
			Actual	Standardized		
August 14–19	126	0	—	—	—	—
September 9–15	135	0	—	—	—	—
October 17–23	180	13	75	72,8	5,6	8,1
November 10–18	180	17	247	241,4	14,2	26,8
December 10–18	180	14	490	487,2	34,8	54,1
January 12–20	180	5	26	25,5	5,1	2,8
February 6–14	169	4	20	20,4	5,1	2,3
March 27–April 4	175	10	53	53,0	5,3	5,9

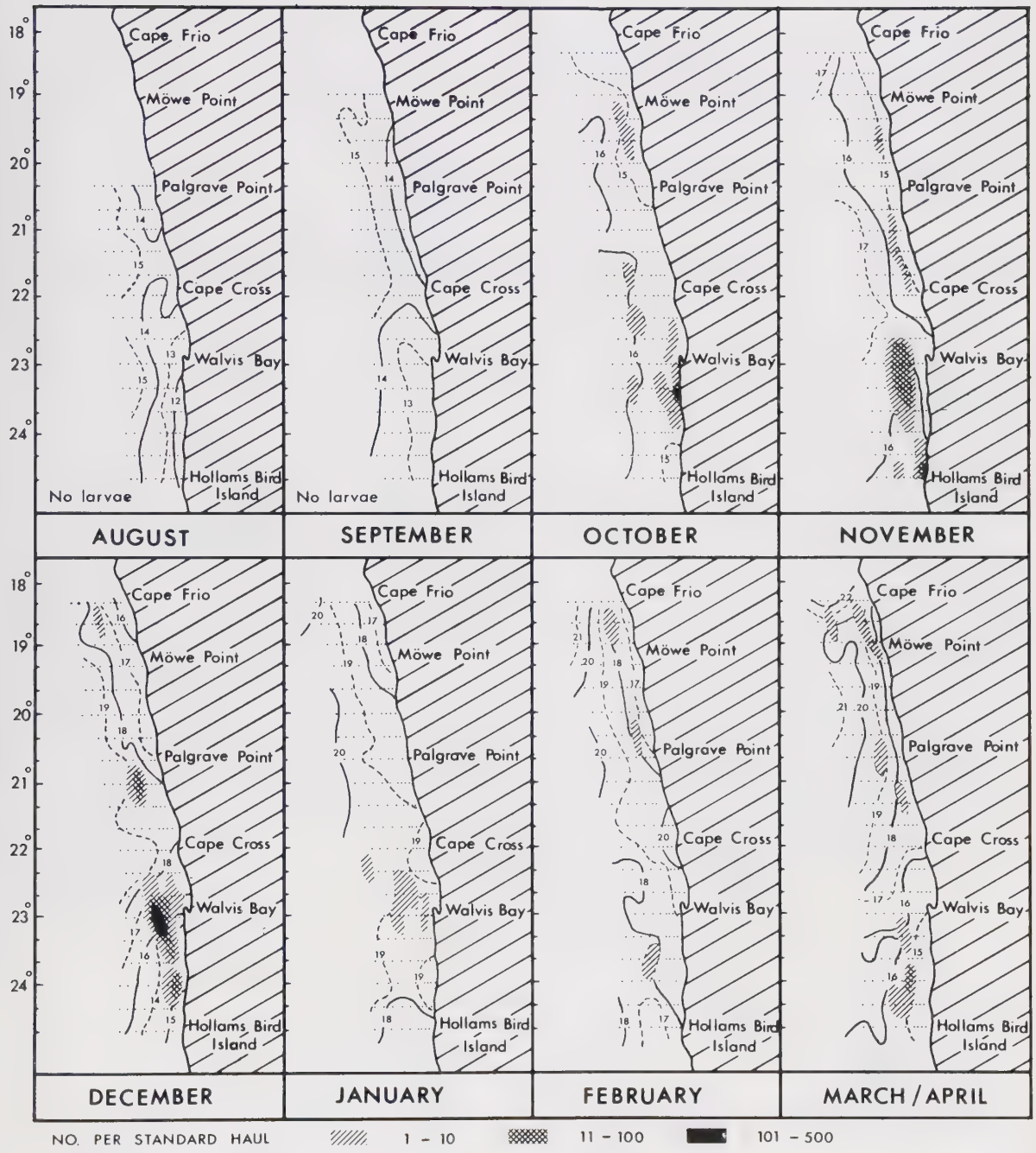

Fig. 6: Monthly distribution and abundance of hake larvae, August 1973 to March/April 1974

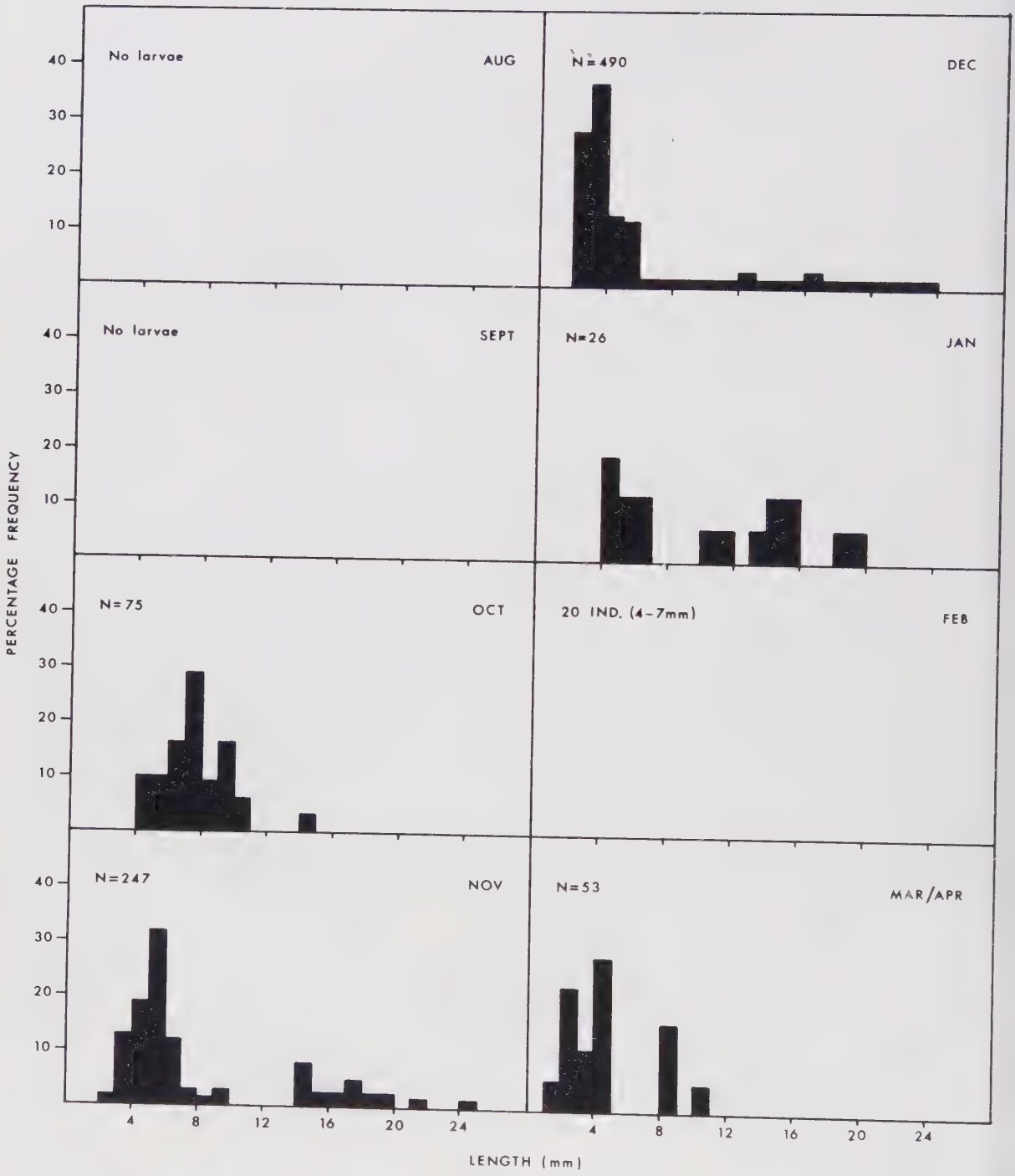

Fig. 7: Length composition of hake larvae collected during the survey cruises August 1973 to March/April 1974

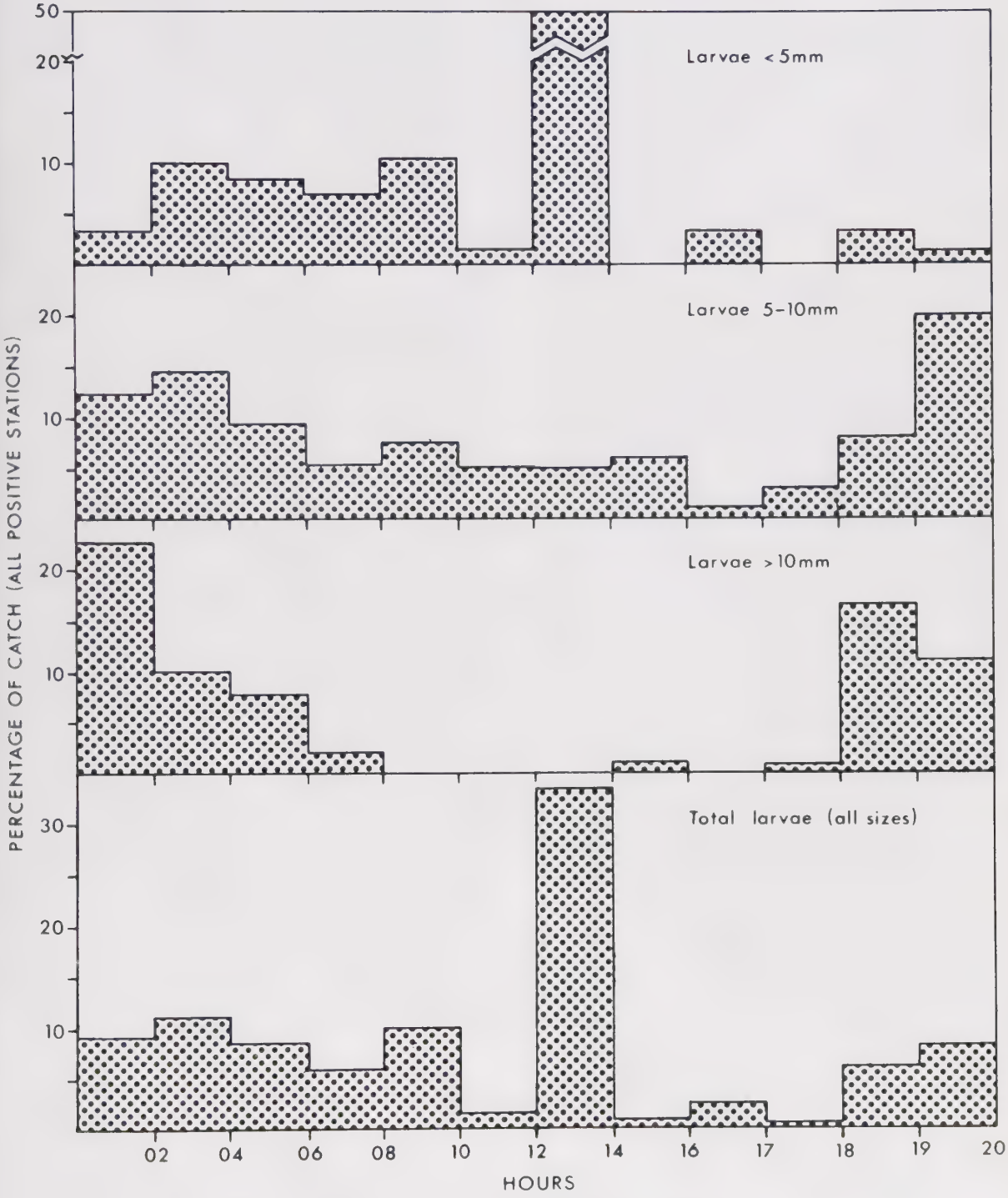

Fig. 8: Diurnal variation in the catch rate of hake larvae according to size categories (all cruises)

Table VI: Day and night catches of different size larvae

Size group (mm)	Positive day hauls (N = 58)		Positive night hauls (N = 57)		Day : Night
	Number of larvae	Percentage	Number of larvae	Percentage	
≤5,0	328	74,9	110	25,1	3 : 1
5,1 – 10,0	55	35,5	100	64,5	1 : 2
10,1 – 15,0	7	7,5	87	92,5	1 : 12
>15,0	19	18,4	84	81,6	1 : 5
Total	409	51,8	381	48,2	1 : 1

collections made at night.

Occurrence of larvae in relation to temperature

The relationship between abundance of larvae and surface temperature is summarized in Table VII. Hake larvae were found where surface temperature ranged from 12,6°C to 19,9°C. Almost 60 per cent of all positive hauls were made at temperatures between 14,8°C and 16,5°C. Approximately 13 per cent of the positive hauls were made at surface temperatures higher than 18°C and 19 per cent at temperatures lower than 14°C. The optimal temperature range is similar to that found by Porębski and Koronkiewicz (1975) who reported that hake larvae collected during summer between Cape Frio and the Orange River occurred at mean surface temperatures between 15,2°C and 15,9°C.

Variation in the depth distribution of larvae was not studied; consequently, a precise temperature-catch relationship could not be determined except in vertically isothermal conditions. The vertical distribution of larvae of other hake species has been studied. Ahlstrom and Counts (1955) and Ahlstrom (1959) found that larvae of the Pacific hake *Merluccius productus* were most abundant near or within the thermocline. Fahay (1974) reported that larvae of the silver hake *M. bilinearis*, during summer, apparently also concentrated near the thermocline.

The depth of the thermocline in localities where hake larvae were found during this investigation varied from 15 m to 30 m (O'Toole 1977a). If 20 m represents the average depth of the thermocline and larval abundance is related to temperature at this depth, then 50 per cent of the hauls containing larvae were made at temperatures higher than 15°C and 25 per cent at temperatures lower than 13°C. The relationship between abundance and temperature at 20 m is given in Table VIII.

In order to test whether larval abundance was significantly related to temperature, the Kruskal-Wallis one-way analysis of variance by rank (Siegel 1956) was applied to the original data summarized in Tables VII and VIII. H° values of 18,58 and 21,38 were obtained for temperature ranges at the surface and at 20 m respectively, indicating significant differences in each case ($P < 0,01$). A possible indication that hake larvae were predominantly located at a depth of 20 m could be inferred from H° values, since there

Table VII: Relationship between surface temperature and abundance of hake larvae

Surface temperature (°C)	Number of standard hauls that collected:					Total positive hauls
	1–5 larvae	6–10 larvae	11–100 larvae	101–250 larvae	251+ larvae	
12,1–13,0	3	2	0	0	0	5
13,1–14,0	7	7	3	0	0	17
14,1–15,0	11	3	8	0	0	22
15,1–16,0	10	5	7	0	0	22
16,1–17,0	16	3	1	1	1	22
17,1–18,0	7	2	3	0	0	12
18,1–19,0	9	1	0	0	0	10
19,1–20,0	3	2	0	0	0	5

Table VIII: Relationship between water temperature at 20 metres depth and abundance of hake larvae

Temperature at 20 m (°C)	Number of standard hauls that collected:					Total positive hauls
	1–5 larvae	6–10 larvae	11–100 larvae	101–250 larvae	251+ larvae	
10,1–11,0	3	1	0	0	0	4
11,1–12,0	3	0	3	0	0	6
12,1–13,0	11	6	1	0	0	18
13,1–14,0	15	10	8	0	0	33
14,1–15,0	13	5	5	1	1	25
15,1–16,0	9	3	4	0	0	16
16,1–17,0	6	0	1	0	0	7
17,1–18,0	5	0	0	0	0	5
18,1–19,0	1	0	0	0	0	1

was a better temperature-dependence at 20 m than at the surface.

Occurrence of larvae in relation to salinity

Hake larvae occurred over a surface salinity range of 34,89‰ to 35,70‰. However, 85 per cent of the hauls containing larvae were found in relatively low-salinity water ranging from 34,90‰ to 35,20‰. Approximately 10 per cent of positive hauls were made in water of salinity less than 34,90‰ and only 5 per cent at salinities greater than 35,20‰ (Table IX). Larval abundance could not be related to depth and salinity because no vertical distribution of salinity was available.

Relationship between larval distribution and hydrography

The present discussion is confined to a general outline relating the seasonal abundance and distribution of hake larvae to hydrographical changes in the spawning grounds south of Cape Cross. For the purpose of analysis, it is assumed that major hydrological change did not occur between survey cruises and that the transition from one month to the next was a gradual one.

Table IX: Percentage frequency of positive hauls in relation to surface salinity

Salinity range (‰)	Number of positive hauls	Frequency (%)
34,81–34,90	3	2,6
34,91–35,00	12	10,4
35,01–35,10	52	45,2
35,11–35,20	35	30,4
>35,20	13	11,3

The gross movements of water masses can be traced from the horizontal distribution of surface temperature outlined on the larval distribution charts (Figs. 4 and 6). However, a detailed account of the seasonal hydrographical features including temperature-depth profiles for both surveys is given by O'Toole (1977a).

Survey 1 (August 1972 to March 1973) – No hake larvae were found in the plankton during the strong upwelling months of August and September, but sampling was not carried out north of 20°S. The vertical distribution of temperature along the Walvis Bay and Hollams Bird Island lines showed conditions typical of late winter and early spring, with cold water (11–14°C) widespread and temperature isothermal in the upper 50 m. In October, upwelling was still persistent and larvae were recorded in small numbers off Walvis Bay.

In November, upwelling slackened considerably, 16°C water advanced inshore and hake larvae became more plentiful. Larval concentrations were found mainly in the relatively cold, 14–15°C mixed water inshore near Walvis Bay. Peak abundance occurred in December when temperature increased because of substantial intrusions of warm water in the north. The more stratified warmer waters north of Walvis Bay formed a well-defined boundary zone with the cooler coastal waters further south. Highest densities of larvae were found off shore north-west of Walvis Bay in the region of mixing between 16°C water and 18°C water.

The number of hake larvae declined sharply in January and they remained relatively scarce during late summer and early autumn (February to March). Hydrographical conditions indicated

that, during this period, high temperatures and well-established thermoclines prevailed in the spawning grounds.

Survey 2 (August 1973 to March/April 1974) – During 1973, no hake larvae were caught during August or September, but sampling was again incomplete in the north. Upwelling was strong over the whole area and conditions were similar to those encountered during the same months of 1972.

By October, however, upwelling had weakened considerably, resulting in a marked intrusion of warm, 16°C water into the spawning grounds. Thermoclines were well developed, particularly inshore in the upper 25 m. Further off shore, mixing was taking place between the warmer, 16°C water pushing eastward and the cooler, subsurface 14°C water moving off shore. Hake larvae were common during October inshore south of Walvis Bay, predominantly between the 15°C and 16°C surface isotherms.

By November, 16°C water had advanced further shorewards and southwards over the spawning grounds. Larvae increased in abundance but were found further off shore in the mixing zone between the warmer, 16°C, oceanic water and the cooler, 14°C, subsurface water.

In December, temperatures north of Walvis Bay had increased owing to an influx of 17°C and 18°C water. The intrusion formed a well-defined boundary zone with the colder, upwelled water in the south. Hake larvae were taken in greatest numbers during this month. Highest densities occurred west of Walvis Bay in the region of mixing between the warm and cold water masses.

Larval abundance declined sharply in January, the decrease coinciding with higher temperatures and marked thermal stratification in the upper 15 m. Hydrographical conditions in February were similar to those in January and larvae were noticeably scarce. Larvae reappeared during March/April and were more abundant in the south, following a drop in temperature and an increase in upwelling.

Dispersal of larvae

The drift of newly hatched hake larvae would depend directly upon oceanographic conditions, particularly the movement of currents during and shortly after spawning. An examination of Figures 4 and 6 shows that the peak spawning months of both years (November and December) in general coincided with a period when warm water pushed southwards and shorewards over the spawning grounds against cold north-flowing Benguela water. The regional distribution of hake larvae during these months changed little, suggesting that developing larvae remained in the vicinity of Walvis Bay, possibly being confined there by the intrusions of warm water.

It is not possible to illustrate dispersal within the gross spawning area from the monthly differences in size-class distribution, because both large and small larvae were frequently taken together in individual samples. However, larvae captured in November 1972 were mostly recently hatched and occurred close to the coast near Walvis Bay (Figs. 4 and 5). In December, specimens taken in the samples were considerably larger and were concentrated further off shore, north-west of Walvis Bay. Thus, a slight off-shore movement of larvae between the cruises in these months is suggested. Although a comparison of surface temperature patterns showed an influx of relatively warm water between November and December, vertical temperature profiles off Walvis Bay indicated a weak off-shore displacement of subsurface water at depths of 20–30 m, which may have carried the developing larvae in a north-west direction. During the same period in 1973, there was no evidence of larval dispersal within the main spawning area (Fig. 6).

Catches of larger larvae were occasionally made in the south, especially in November, near Hollams Bird Island, suggesting that these advanced stages may have been carried northwards from spawning centres south of the research area.

Age of larvae

A basis for roughly determining the growth rate of larvae at sea and from it estimating the age of a larva of a given size can sometimes be established by tracing the movement and progressive increase in size of specimens captured in a given area over a relatively short period of time. In the case of hake, it was only possible to trace a cohort of developing larvae between November and December 1972 when but a slight drift off shore was apparent. The length frequency curves for larvae collected at stations within the main spawning area, i.e. lines 66, 70 and 74 (Fig. 1), for both months are shown in Figure 9.

In November, a major cohort consisting of recently hatched larvae between 3 mm and 6 mm

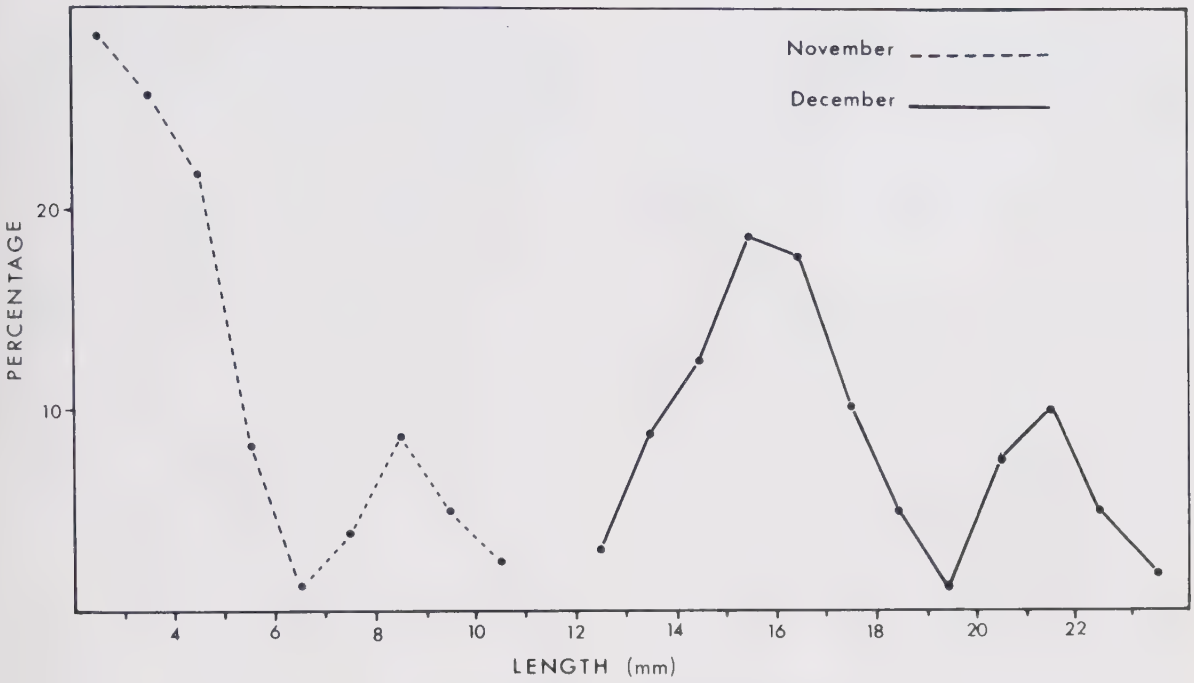

Fig. 9: Length frequency curves for larvae collected off Walvis Bay in November and December 1972

in length (mean 4,0 mm) and a smaller group of larger specimens between 7 mm and 10 mm in length (mean 8,0 mm) were identified. During the December cruise, catches of larger larvae made in the same general area, but further off shore, also showed two size-frequency peaks, a large cohort of specimens from 14 mm to 18 mm in length (mean 16,0 mm) and a less dominant group 19–22 mm in length (mean 20,0 mm). If the two groups of recently hatched larvae collected near Walvis Bay in November (Fig. 4) were represented by the two older cohorts taken off shore in December, as hydrographical interpretations suggest, then it is possible to estimate the growth rate. The mean length of larvae in the two cohorts increased from 4 mm to 16 mm and from 8 mm to 20 mm respectively during the intervening period, representing an increase of 12 mm in 26 days or an average growth rate of about 0,45 mm per day for each cohort.

DISCUSSION

The area between Henties Bay and Hollams Bird Island is an important spawning ground of the hake. The occurrence of newly hatched larvae suggests that spawning was continuous from September to April. However, the majority of fish apparently spawned between October and December (mid-spring to early summer) during the two years studied. Newly hatched larvae predominated off Walvis Bay 50–100 km off the coast. The northward and seaward limits of the spawning grounds were adequately encompassed, but spawning may also have occurred further south, because small larvae were sometimes abundant on the most southerly line of stations. These interpretations are supported by evidence of the distribution of sexually mature hake (Chłapowski 1975) and of egg occurrence and seasonal abundance (Porębski and Koronkiewicz 1975).

In January of both years, there was a sharp decline in hake larval abundance, indicating that the spawning season may be relatively short and spawning almost complete by that time of the year. However, the occasional appearance of newly hatched larvae in the plankton during summer, and then especially in the north, indicates that some fish spawn later.

Approximately 70 per cent of the newly

hatched hake larvae were collected during full daylight whereas larger specimens were mainly taken at night. Fahay (1974) reported similar findings for larvae of the silver hake *M. bilinearis*. The most generally accepted explanation for the high incidence of large larvae in night hauls is that the more advanced stages can avoid slow-moving collecting gear more effectively during daylight in response to visual warning.

Diurnal vertical migration, although not studied during this investigation, might have contributed to the disparity between day and night catches. However, Ahlstrom (1959) reported that larvae of Pacific hake *M. productus* had a similar depth range in both day and night hauls, and Fahay (1974) noted that the larger silver hake larvae displayed only limited diurnal vertical migration in the upper 33 m of water. It is, therefore, probable that the differences in catch rate can mainly be attributed to avoidance.

The consistently greater abundance of newly hatched larvae in hauls made during daylight could be due to aggregation behaviour in response to food and light.

Monthly fluctuations in the abundance of small larvae suggested that the intensity and the timing of hake spawning differed between years. For example, the main spawning season commenced a month earlier during survey 2 than during survey 1. Hake larvae first appeared in the plankton when upwelling was weakening and temperatures higher. In October 1972 the water temperature in the spawning grounds remained relatively low because of persistent coastal upwelling.Newly hatched larvae were noticeably scarce during this month, suggesting little spawning activity. In contrast, upwelling was much reduced in October 1973, resulting in higher temperatures and the establishment of thermoclines in the shallow layers near the coast (O'Toole 1977a). Early larval stages were correspondingly more abundant, which suggested that heavy spawning was induced earlier, possibly because favourable biotic or abiotic conditions were reached more rapidly.

Conditions and spawning patterns during summer and autumn were essentially similar in both surveys. During November and December, catches of hake larvae reached a peak at a time when warm water intruded southwards and shorewards in the vicinity of Walvis Bay. The sharp boundary zone between these intrusions and the cooler coastal water off Walvis Bay appeared to be the focus of heavy spawning. The end of the main breeding season was marked by increasingly high temperatures and the formation of strong temperature gradients inshore. However, some isolated spawning continued to take place during late summer and early autumn where the environment was temporarily suitable, e.g. south of Walvis Bay in March/April 1974 (Fig. 6), following a drop in temperature associated with an intensification of upwelling and mixing.

Continuous spawning from October to December caused difficulties in tracing the dispersal of developing hake larvae. Hydrographical evidence suggested that there was little or no transportation northwards and only a slight movement off shore. The months of heaviest spawning generally coincided with the period when the north-flowing Benguela Current weakened and movements of warm off-shore water southwards and towards the coast took place. The interaction of these two water masses off Walvis Bay appeared to contain developing larvae within the main spawning area, thereby allowing them to remain in the productive coastal environment.

The time taken for larvae to complete their development will depend directly upon temperature and food availability. Larvae of *M. capensis* develop juvenile features and possess a full complement of fin rays at a length of about 25 mm. A rough estimate of the pelagic phase of development would be $1\frac{1}{2} - 2$ months. Although juvenile hake 25–35 mm long were collected at night on several occasions (O'Toole 1976), the location of capture (south of Walvis Bay) also indicated that there was little emigration of juveniles out of the general breeding area.

There was no evidence from this study of a horizontal spawning migration of hake off South West Africa. The facts that on the research cruises, international vessels exploiting hake were observed on the traditional fishing grounds (i.e. Cunene River to Palgrave Point and Walvis Bay to Conception Bay) during most of the year and that no mention of fleet redeployment has been made in specific reports, mainly those published by the International Commission for the South East Atlantic Fisheries (ICSEAF), lend support to this argument. Furthermore, the sudden appearance of larvae in the vicinity of Walvis Bay during October and November and the fact that distributional patterns of recently hatched larvae suggest no noticeable seasonal movement of spawning fish imply that hake simply spawn wherever they are concentrated, provided environmental conditions are suitable. In Cape waters, Botha (1973) found little evidence of hake spawning migration from catch data and suggested that, during the spawning season, hake merely rise to midwater to spawn wherever they are concentrated.

The hake stocks fished in the northern waters of South West Africa appear to be a separate population. According to Draganik (1976), the total hake landings in ICSEAF division 1.3 (15–20°S) are practically equal to those in division 1.4 (20–25°S). However, in the present study little evidence of spawning activity was found in the north. During summer and early autumn, the northern off-shore waters are important spawning areas for other fish species (O'Toole 1977b, 1977c, 1977d) and seem to be particularly favourable as a nursery area for their larvae.

The presence of some recently hatched hake larvae in this region during summer and autumn, although they were few in contrast to the number derived from the earlier spawning in the south, does indicate that the northern stock may be predominantly summer-autumn spawners. An explanation of this lack of spawning activity in the north may be, either that hake breed outside the limits of the survey area, or that many of the eggs and larvae occur at depths below 50 m where they are consequently out of reach of the sampling gear. Another possibility is that the northern population may spawn mainly from mid-autumn to winter, a period not covered during this investigation.

The information contained in this report was collected incidentally during a survey aimed at other species. Also, hake is of vital commercial importance around the whole of southern Africa. For these reasons, it is desirable to undertake a more complete survey covering the geographical distribution of the early stages and to back this up with laboratory observations on the effects of environmental factors on embryonic and larval development.

ACKNOWLEDGEMENTS

Special thanks are due to Mr C. J. Giddey and Mrs S. M. Payne for their help in sorting plankton. The comments and advice received from Mr L. Botha, Dr J. Field (University of Cape Town), Mr A. I. L. Payne and Mr P. Shelton are gratefully acknowledged.

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This report is based on a section of a dissertation submitted in April 1977 as part requirement for the degree of Doctor of Philosophy at the University of Cape Town.

Fish. Bull. S. Afr. 10:37–45
1978

LABORATORY OBSERVATIONS ON THE EARLY DEVELOPMENT OF THE ANCHOVY *ENGRAULIS CAPENSIS* FROM THE CAPE PENINSULA

D. P. F. KING, A. A. ROBERTSON and P. A. SHELTON

The main components of the South African, multispecies, purse-seine fishery are the pilchard *Sardinops ocellata* Pappe, the maasbanker (horse mackerel) *Trachurus trachurus* L. and the anchovy *Engraulis capensis* Gilchrist. As these species occupy similar ecological niches in the pelagic environment, at least for part of their life histories, competition could be reduced by behavioural and physiological differences. Their spawning patterns frequently coincide geographically and seasonally. It is possible that differences in thermal limits to spawning and in temperature-specific development rates lessen interaction between these species. To date, information on the early life history of the anchovy *E. capensis* has been restricted to observations on the distribution of eggs and larvae in nature (Anders 1965, 1975).

In the present report, the development of the anchovy from early cleavage stages in the ova to larvae at the stage of jaw formation and eye pigmentation is described, and the effect of temperature on the rate of development is shown.

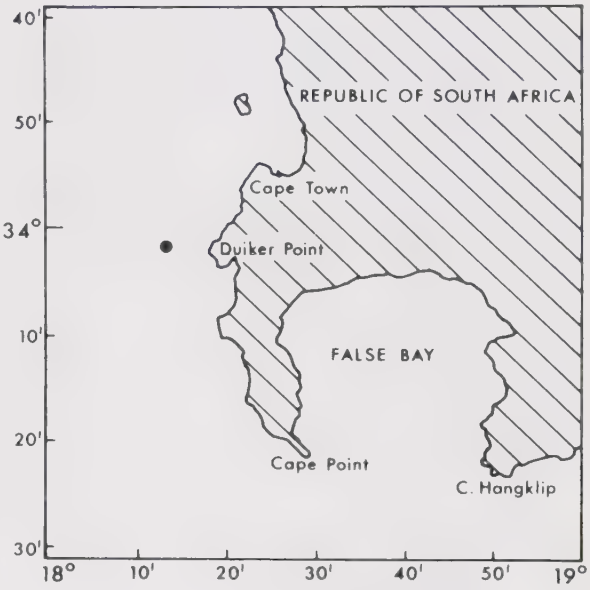

Fig. 1: Location of capture of eggs

MATERIAL AND METHODS

Eggs were collected by means of an EES-52 plankton net (King and Robertson 1973) towed at the surface from the research ship *Benguela* at 11h00 on 7 December, 1976. A single haul was made at a position 6 km due west of Duiker Point (Fig. 1). On retrieval, the codend of the net was placed in a 10-*l* rubber bucket and the contents gently rinsed down with sea water. After partial concentration of the sample, anchovy eggs were removed and separated into their different developmental stages. A total of 969 eggs were removed, of which 53 per cent were in the early blastula stage. At the time of collection the sea surface temperature was 18°C.

In order to measure the time-lapse to the various embryological stages over a wide range of temperatures, a thermal-gradient incubator as described by King (1975) was employed.

On board ship, 2–3 eggs at the blastodisc stage of development were placed in each incubator tube in the first two rows of the block. Each tube contained 100 m*l* filtered sea water from the same general area previously equilibrated to the temperature of the block position. To assist in monitoring the length of time to the various biological events such as hatching and jaw formation, two supplementary samples of between 6 and 9 eggs were incubated at the different experimental temperatures in two of the other rows of the block. A range of 12,45 deg C (10,76–23,21°C) was maintained throughout the experiment. Temperature was monitored hourly with a 12-channel scanning thermistor recorder; fluctuations during the experiment were small, standard deviations being 0,09–0,95 deg C (Table I).

Individual eggs from the first two rows of the incubator block were removed every 2–4 hours and placed in a staining block. Supplementary supplies of filtered sea water at the correct temperature were available in the sixth row of the

Table I: Mean temperature and standard deviation for each row of incubator tubes

Row No.	Mean temperature (°C)	SD
1	23,21	0,15
2	22,15	0,10
3	20,89	0,17
4	19,46	0,09
5	17,90	0,88
6	16,46	0,95
7	15,01	0,15
8	13,59	0,13
9	11,90	0,19
10	10,76	0,28

incubator block. After brief microscopic examination they were returned to their appropriate incubation tubes. Bulk samples were only examined when hatching was imminent in order to determine the precise time of hatching.

Initially, larvae were observed every 6–12 hours and thereafter every 24 hours until complete yolk absorption and eye pigmentation had been effected. To facilitate measurement, the larvae were anaesthetized by placing in a seawater solution of MS 222 at a concentration of 1:20 000 (mass/volume). These solutions, equilibrated to the correct temperatures, were kept available in the fifth row of the incubator block. An ocular micrometer was used to measure the larvae to the nearest 0,01 mm from the tip of the snout to the posterior end of the notochord.

RESULTS

Development of the egg

The eggs of *E. capensis* (Fig. 2) are pelagic. They are typical engraulid eggs in that they are ovoid, possess a smooth chorion, a narrow perivitelline space and segmented yolk and have no oil globule. Measurements of the major and minor axes at various stages of development (Table II) showed no size difference in the eggs at the different stages.

Although no detailed description of the embryonic development of *E. capensis* has been published, the embryology of related species has been well documented (Bolin 1936, Ahlstrom 1956 and De Ciechomski 1967). Because the development of all engraulid eggs is basically similar, only a brief description is given here. The development of the Cape anchovy egg can broadly be classified into three phases: early (fertilization through to blastopore closure), middle (blastopore closure to the point where the tail separates from the yolk) and late (tail separation to hatching).

Early phase (Figs. 2A-2C) – In the youngest stage observed, several cleavages had already taken place, resulting in the formation of a high blastodermal cap. With repeated cleavage the blastomeres become smaller and the blastodermal cap assumes a lenticular dome shape (Fig. 2A). Subsequently, the entire peripheral rim of the blastoderm thickens to form the germ ring. The embryonic shield is then visible, particularly when the egg is viewed dorsally (Fig. 2B), and along the median line the embryonic axis becomes evident (Fig. 2C). Just before the blastopore closes, a few somites appear half way along the body of the embryo.

Middle phase (Fig. 2D) – Shortly after blastopore closure, the eyes, though rudimentary, are discernible and Kupffer's vesicle appears at the posterior end of the embryo (Fig. 2D). By the end of this phase, the tip of the tail is no longer flattened but has become swollen, still, however, adhering to the surface of the yolk. Kupffer's vesicle has disappeared and the eye lenses are clearly visible. After the disappearance of Kupffer's vesicle, the tail bud separates from the yolk.

Table II: Egg diameter at three developmental stages

Developmental stage	Number measured	Mean diameter (mm)*					
		Major axis	Range	SD	Minor axis	Range	SD
Blastodermal cap	50	1,42	1,28–1,61	0,09	0,62	0,44–0,64	0,04
Tail separation	50	1,42	1,19–1,59	0,08	0,61	0,56–0,66	0,04
Hatching imminent	50	1,42	1,30–1,59	0,08	0,60	0,52–0,67	0,05

* Eggs measured after preservation in 5 per cent formalin

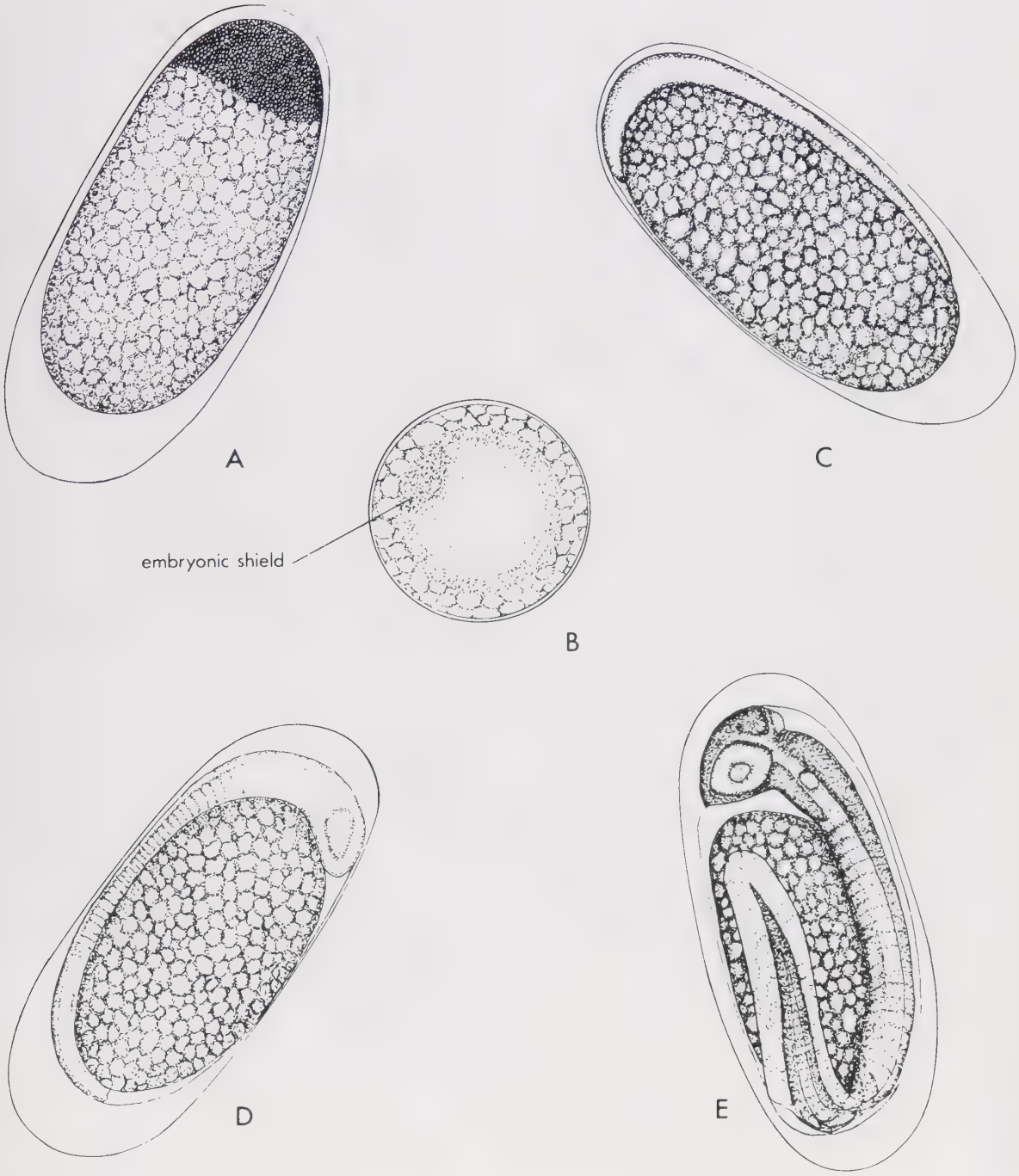

Fig. 2: Eggs of *Engraulis capensis*. A, B and C – early phase; D – middle phase; E – late phase

Late phase (Fig. 2E) – Development during this phase is largely characterized by the degree of tail development. As the tail lifts off the yolk and begins to twist out of the embryonic axis, the fin fold is apparent on the ventral edge of the tail. Simultaneously, the eyes and the main divisions of the brain become clearly defined. The auditory capsules appear and the full length of the digestive tract and the position of the vent are discernible at this stage. More somites differentiate along the tail as it twists further, and the fin fold broadens and extends around the body from the back of the head (Fig. 2E). Prior to hatching, the heart begins beating, the tail is flexed well over the body though not reaching the level of the head and 28–30 somites develop posterior to the vent. Body movements become frequent but there is no intrachorional somersaulting.

Embryonic development rates

Only the period from formation of the blastodermal cap to hatching was observed because no earlier stages were caught in the plankton tows.

At 10,76°C, development did not proceed beyond germ ring formation. At temperatures below 13,59°C, development proceeded slowly to hatching (95h at 11,90°C), but subsequent larval development was abnormal and characterized by pronounced spinal curvature. Regression diagrams were used to describe the relationship between temperature and time to several morphological events (Fig. 3). The expression used was of the form $y = ax^b$ where y = incubation time (hours), x = temperature (°C), and a and b are constants. The calculated regression formulae are given in Table III.

Length of time to the various stages of development during the incubation period was exponential. At the lowest and highest successful incubation temperatures (11,90°C and 23,21°C), complete gastrulation required 54 and 10 hours respectively, and the time to hatching 108 and 21 hours respectively.

Description of the larva

Unlike many other pelagic fish, the anchovy does not develop pigmentation during the egg phase. Newly hatched larvae of *E. capensis* are virtually transparent and the mouth is not developed (Fig. 4A). The yolk sac is large (anterior-posterior length greater than 50 per cent of the total length of the larva). The head of the larva at hatching is initially curved over the top of the yolk sac. Cupulae of neuromast organs are clearly discernible as a row of 5–6 spinelike projections along each side of the body, but are not visible on preserved specimens.

As yolk absorption progresses, the head region straightens and the pectoral fin buds appear. Areas of pigmentation begin to show 1–3 days after hatching. Pigment first appears around the outer margin of the eye. When the larva attains a length of 3,4–3,6 mm, a few elongated melanophores appear along the ventral surface, extending from the anterior origin of the pectoral fin buds to the tail tip (Fig. 4B). In larvae 3,7–3,9 mm long, the yolk has completely been absorbed and the eyes are apparently functional (Fig. 4C).

Growth of the larva

At hatching, the larvae of *E. capensis* were 2,48–3,20 mm in length (Table IV). Analysis of variance showed that the mean lengths of larvae hatched at the 9 different incubation temperatures were not significantly different ($F = 1,20$, $P < 0,05$ with 100 degrees of freedom).

Figure 5 illustrates the change in length of anchovy yolk-sac larvae at three different temperatures, namely 22,15°C, 17,90°C and 13,59°C.

Table III: Regression formulae for the development of eggs incubated at different temperatures

Stage	Number measured	Regression	Correlation coefficient r	Significance level
Blastopore closure	33	$y=37221,76x^{-2,64}$	–0,98	$P < 0,005$
Tail separation	35	$y=34732,12x^{-2,55}$	–0,98	$P < 0,005$
Heart functioning	29	$y=57568,79x^{-2,59}$	–0,98	$P < 0,005$
Hatching	72	$y=43787,93x^{-2,41}$	–0,99	$P < 0,005$

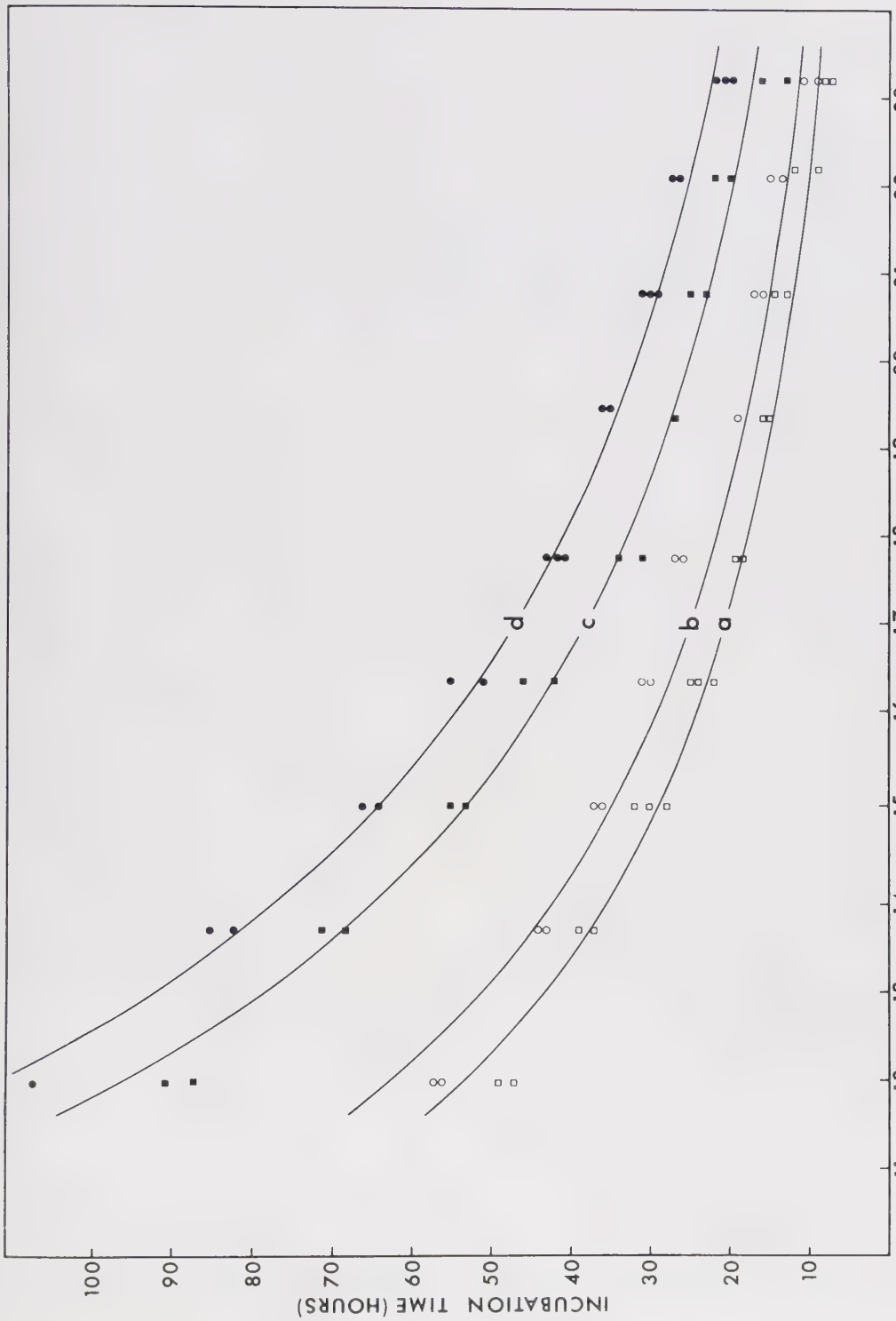

Fig. 3: Incubation times to (a) blastopore closure, (b) tail separation, (c) heart functioning and (d) hatching

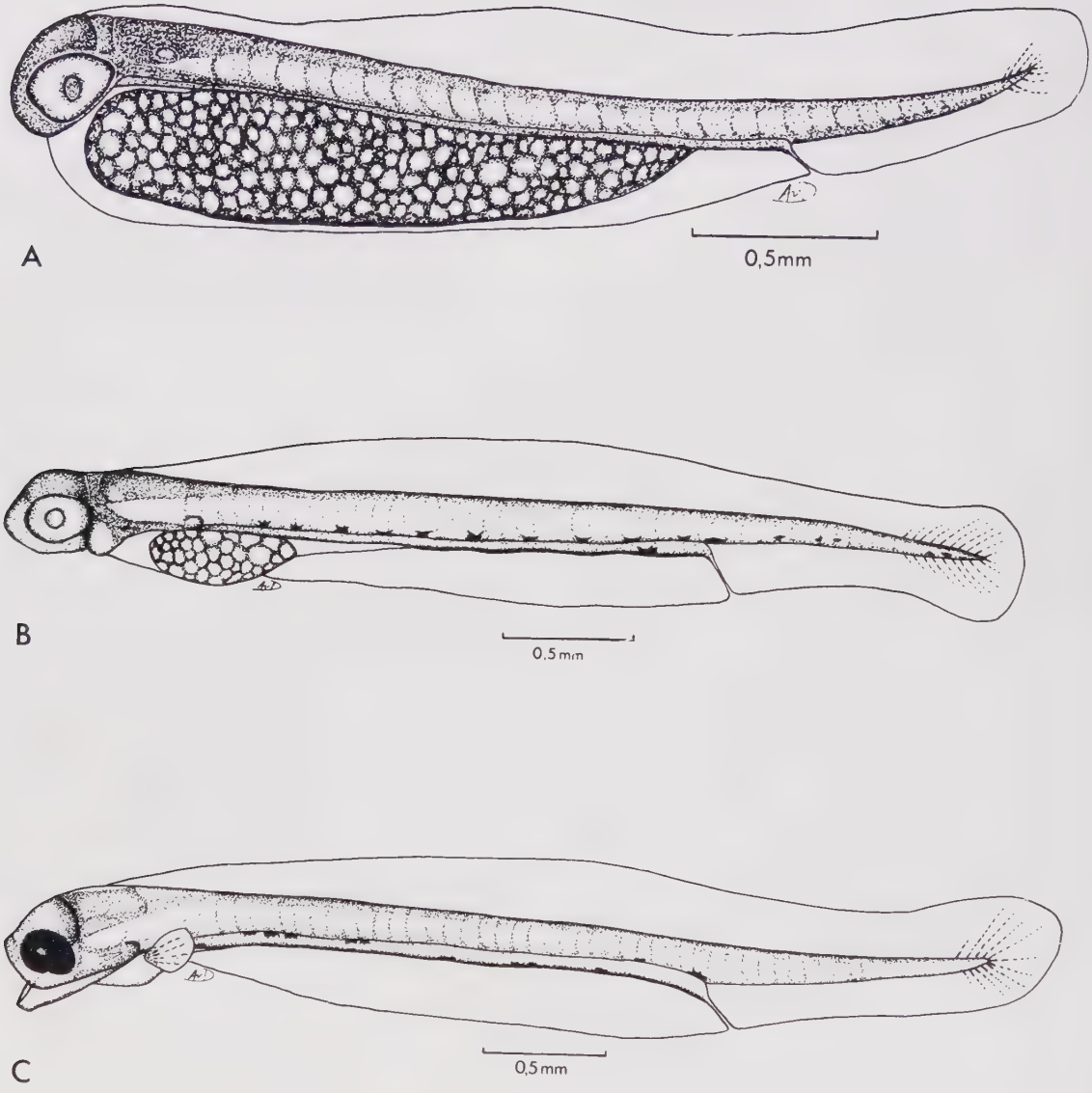

Fig. 4: *Engraulis capensis* larvae. A – newly hatched; 8 – 48 h after hatching; C – 72 h after hatching

Table IV: Notochordal length of newly hatched larvae at nine incubation temperatures

Temperature (°C)	Number measured	Larval length (mm)		
		Mean	Range	SD
10,76	0	—	—	—
11,90	9	2,86	2,66–3,10	0,15
13,59	11	2,90	2,56–3,08	0,16
15,01	10	2,85	2,72–3,12	0,15
16,46	11	2,85	2,56–3,12	0,17
17,90	15	2,80	2,48–3,00	0,17
19,46	13	2,89	2,56–3,16	0,17
20,89	13	2,91	2,72–3,08	0,12
22,15	13	2,77	2,48–3,04	0,18
23,21	14	2,84	2,68–3,20	0,24

The growth points represent the mean size of each sample group for each temperature. Eye pigmentation and jaw formation were complete in 2 days at 22,15°C and in 3 days at 17,90°C. At 13,59°C, anchovy larvae failed to develop pigmented eyes and functional jaws. Regression in size associated with starvation occurred in those larvae reared at temperatures higher than 13,59°C after yolk absorption, while those reared at 13,59°C underwent shrinkage prior to complete yolk absorption. Thus, it appears that larvae reared at a temperature of 13,59°C transformed yolk into body tissue at suboptimal levels. The highest mean length before shrinkage (3,90 mm) was obtained for larvae reared at 17,90°C.

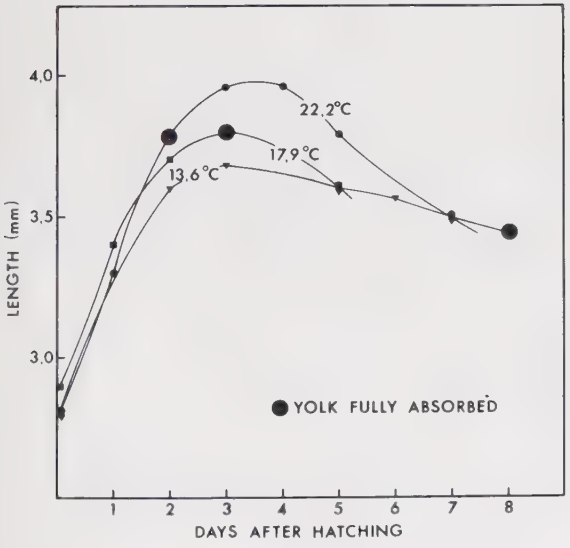

Fig. 5: Change in length of yolk-sac larvae held at three incubation temperatures

DISCUSSION

Developing eggs of engraulids are similar in many respects. Sizes of fertilized eggs of some described species range from 1,15 mm to 1,55 mm along the major axis and 0,65 mm to 0,82 mm along the minor axis (Bolin 1936, De Ciechomski 1967). The major axis of *E. capensis* eggs is within the same range as that of the other species, but the length along the minor axis (0,44–0,67 mm) was smaller.

The newly hatched larvae of the northern anchovy *Engraulis mordax* (Bolin 1936) and of the Argentinian anchovy *E. anchoita* (De Ciechomski 1967) closely resemble those of *E. capensis*. On hatching, larvae are elongated, threadlike and lack pigmentation, but within two days of hatching a series of melanophores is visible along the ventral surface in all three species. The present results indicate that larvae of *E. capensis* hatch at a length of about 2,86 mm, which is similar to the length at hatching for *E. mordax* and *E. anchoita*.

The average incubation periods for *E. capensis* from blastodermal cap stage to hatching (66 and 34 hours at 15°C and 20°C respectively) were considerably longer than those reported for *E. mordax*, which at 15°C hatched in 41 hours and at 20°C in 28 hours (Lasker 1964). At 15°C, hatching of *E. anchoita* occurred approximately 63 hours after blastula formation and, at 20°C, about 48 hours after blastula formation (De Ciechomski 1967).

Eggs of *E. capensis* incubated from the blastodisc stage survived a temperature range of 11,31 deg C (11,90–23,21°C), but normal development was inhibited at 13,59°C and the larvae failed to develop a functional jaw or complete eye pigmentation. From this, it would appear that the threshold temperature for anchovy spawning in Cape waters would be about 14°C. Successful development of anchovy eggs and the subsequent survival of their larvae in nature is partly dependent upon their remaining within an appropriate temperature range. Spawning of *E. capensis*, as indicated from eggs in the plankton, takes place in the upper mixed layers in surface temperatures ranging from 9,5°C to 22°C, the

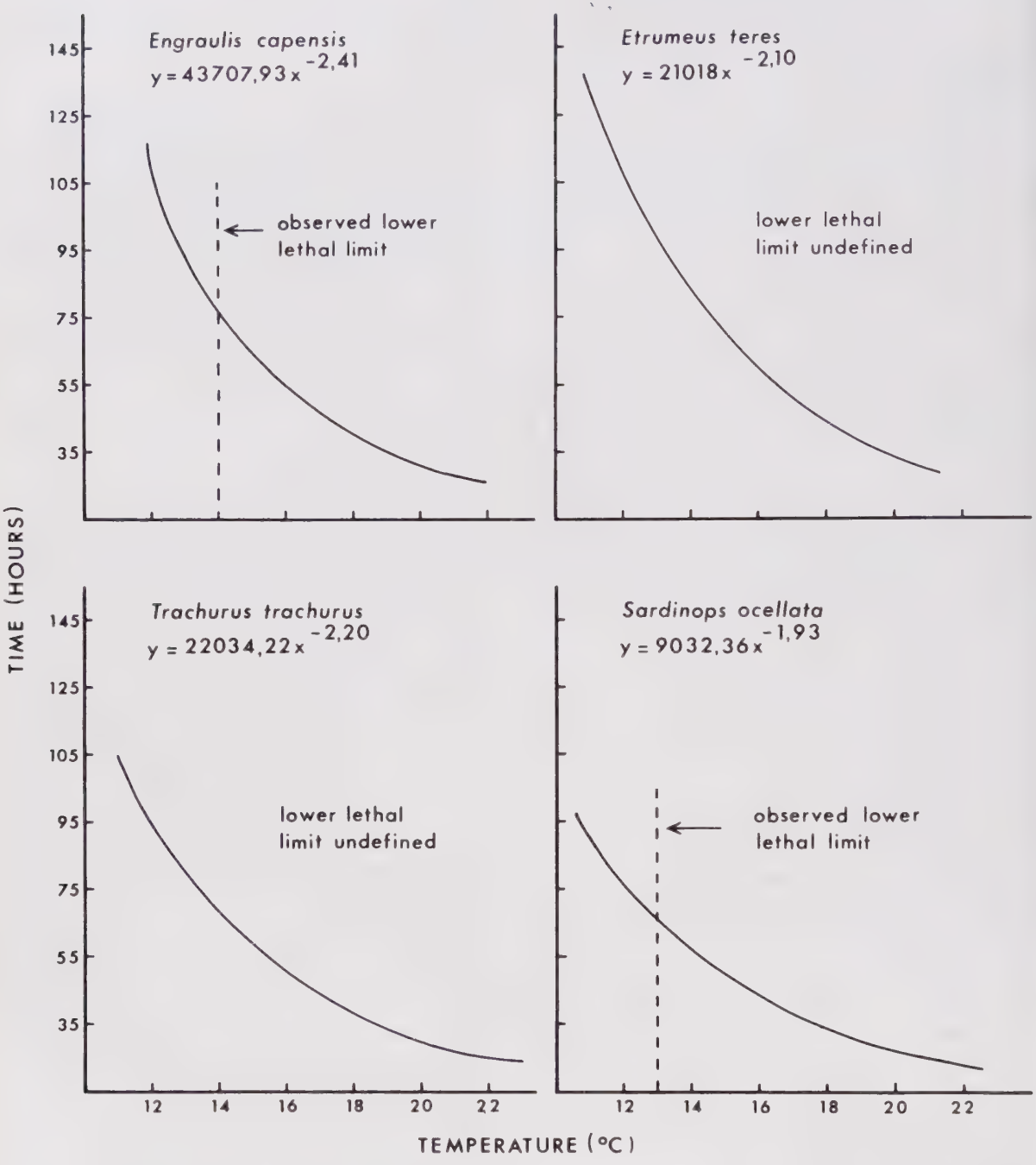

Fig. 6: Estimated incubation periods (blastodermal cap to hatching) for *Engraulis capensis, Etrumeus teres* (O'Toole and King 1974), *Trachurus trachurus* (King *et al.* 1977) and *Sardinops ocellata* (King 1975)

optimum range being 16–19°C (Anders 1965). It would, therefore, appear that anchovy eggs can occur or drift into areas where they are exposed to unfavourable temperatures.

Incubation periods have been determined experimentally for other species commercially important in Southern Africa. These include the round herring *Etrumeus teres* (O'Toole and King 1974) and the maasbanker *Trachurus trachurus* (King *et al.* 1977) in South African waters and the pilchard *Sardinops ocellata* from off South West Africa (King 1975). The effect of temperature on development follows the same pattern in all of these species, i.e. the rate of development increases exponentially with increasing temperature (Fig. 6). Comparison of *Engraulis capensis* with *Etrumeus teres* shows that differences in rates of development are slight, but the anchovy is less tolerant of lower temperature. Incubation proceeds at a slower rate in anchovy than in either maasbanker or pilchard, but the divergence in the rates of development decreases with increasing temperature (Fig. 6).

All the experimental evidence suggests that the anchovy may be at a marked disadvantage with its co-occurring species in the event of an influx of cold water during a spawning season. However, no failure in the anchovy fishery, which depends almost wholly on fish less than one year old, has been recorded since 1965 when full-scale exploitation of anchovy commenced in South Africa.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge the assistance of colleagues in the preparation of this manuscript and express their sincere appreciation to Mr A. P. van Dalsen for illustrating the eggs and the larvae.

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Fish. Bull. S. Afr. 10:46–49
1978

UNUSUAL SEABIRD PREDATION ON HORSE MACKEREL TRAPPED AT HOTTENTOT'S HUISIE, CAPE PENINSULA

P. A. SHELTON, G. DE VILLIERS and R. J. M. CRAWFORD

On 29 September 1977, shortly after a spring tide, a shoal of horse mackerel (maasbanker) *Trachurus trachurus* was observed in a small rocky bay near Hottentot's Huisie, 34°00′S, 18°21′E, by Mr Veldman, a local inhabitant. Although this bay contains large boulders and is exposed to tidal effects, wave action and currents that result in unfavourable water movements and a generally hostile environment, the shoal remained there until at least 6 October, a period of eight days. Seabirds, seals and fishermen caused heavy mortality of the fish during this time. Figure 1 shows a section of the shoal trapped in shallow water, indicating its accessibility to predators.

A total of 200 fish were collected by means of a fine-meshed cast net on the afternoon of 4 October and the morning of the 5th. All were sexually immature and had no food in their stomachs. The total lengths of the fish were fairly

Fig. 1: A section of the shoal of horse mackerel trapped in a shallow pool between large rocks. Some fish (centre) are having difficulty in maintaining their position in the water

Fig. 2: The bay at Hottentot's Huisie where a shoal of horse mackerel was trapped. (a) Cape cormorants, (b) southern black-backed gulls, (c) a pod of Cape fur seals

uniform, ranging only from 19 cm to 23 cm with the mode at 21 cm. According to the von Bertalanffy growth equation for the species (Geldenhuys 1973), the fish were between three and four years old.

Sea-water samples were taken in well-mixed water inside the bay. Because the bay contains a large kelp bed, some of the nutrient values were higher than those encountered in the open sea, but allowing for this fact, all values obtained by later analysis were normal for the time of year. The range of silicate content was 5,8–9,4 µgat/*l*, of phosphate 4,0–4,2 µgat/*l* and of nitrate 19,2–23,4 µgat/*l*, ammonia being constant at 20,45 µgat/*l*. The mean oxygen level was 5,4 m*l*/*l* and the total chlorophyll count 1,29 µg/*l*. The temperature (14°C) was also normal. Three small phytoplankton blooms were noticed about 100 m from the mouth of the bay and examination showed them to consist of *Noctiluca miliaris*, a red-tide species that is normally non-toxic. However, there is no reason to believe that their presence can be associated with the near-stranding of the fish.

Some observations of seabird predation on the shoal were made on the afternoon of 5 October. All birds were counted twice, the average values obtained being 308 Cape Cormorants *Phalacrocorax capensis* and 195 southern black-backed gulls *Larus dominicanus*. Most of the birds were perched on neighbouring rocks and showed little interest in fishing. They seemed to be in a replete condition and two Cape cormorants had fish tails protruding from their mouths. The cormorants favoured the lower outcrops, whereas the gulls were resting at higher levels (Fig. 2). Only about 10 per cent of the cormorants and 20 per cent of the gulls were actively feeding, the latter picking fish off the surface of the water.

In studies conducted between 1952 and 1955, Davies (1955, 1956) only once encountered horse mackerel of a greater length in the stomachs of Cape cormorants. These had a mean total length of 23,7 cm. In all other instances, the average size was less than 10,0 cm. Rand (1960) found no horse mackerel longer than 15 cm in Cape cormorant stomachs collected between 1954 and 1956. The mean size of all prey occurring in the stomachs of Cape cormorants shot in South African waters was 10,5 cm in 1953/1954 and 9,9 cm in 1954/1955 (Crawford and Shelton, in prep.). The birds at Hottentot's Huisie were thus consuming a larger size of fish than is normally the case for Cape cormorants in South African waters, an occurrence no doubt precipitated by the near-stranding of the horse-mackerel shoal. At Walvis Bay, South West Africa, the mean length of fish in Cape cormorant stomachs between 1957 and 1958 was comparable at 19,7 cm (Crawford and Shelton *op.cit.*).

Fishing by southern black-backed gulls is an uncommon activity and may be attributed to the abnormal situation and the opportunistic feeding behaviour of these birds (Watson 1975). Noticeable was their obvious preference for live fish, as horse mackerel dumped on the shore by fishermen were left intact.

A pod of Cape fur seals *Arctocephalus pusillus* comprising approximately 100 individuals was present at the site throughout the observation period, but again only a few of these were observed to be feeding. This is probably because the others were satiated. It is well known that horse mackerel constitute an important component of the Cape fur seal's diet (Rand 1959).

How the shoal of horse mackerel came to be positioned in the bay is not clear, but their immature state and empty stomachs indicate that it was not for the purposes of spawning or feeding. The environmental conditions appeared to be normal. It is possible that they were driven towards the shore by the seals and that wave action was subsequently responsible for landing many of them in small rocky pools. Baird (1971) suggests that a similar mechanism could be responsible for the stranding of pilchards on the beaches of Natal during the "sardine run". Once in the bay, the seals at its mouth may to some extent have prevented escape by the horse mackerel.

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1978

CATCH COMPOSITION AND POPULATION STRUCTURE OF THE COMMERCIALLY EXPLOITED MACKEREL *SCOMBER JAPONICUS*, 1954 – 1975

D. BAIRD

In South Africa, the commercial exploitation of pelagic fish commenced on a small scale in 1943. The fishery originally depended upon two species, the pilchard *Sardinops ocellata* and the maasbanker (horse mackerel) *Trachurus trachurus*, fishing being concentrated mainly in the vicinity of St Helena Bay on the West Coast. Before 1950, no comprehensive catch statistics were kept, but Du Plessis (1959) estimated the catches to consist of approximately 50 per cent pilchard and 50 per cent maasbanker. After 1950, the fishery continued to expand and detailed catch statistics were maintained.

Mackerel *Scomber japonicus* Houttuyn was first recorded in the catches in 1954 although negligible quantities may have been caught in earlier years. Regular but fluctuating catches have since been made. In 1964, the introduction of a smaller-meshed net initiated a larger-scale exploitation of anchovy *Engraulis capensis* and round herring *Etrumeus teres*. During later years the lantern-fish *Lampanyctodes hectoris* also appeared in the catches (Centurier-Harris 1974). The South African, pelagic, purse-seine fishery is thus a truly multispecies one, involving no less than six species.

Table I: Annual total pelagic catch and mackerel catch, 1954 – 1975

Year	Total catch (thousands of metric tons)	Mackerel catch (thousands of metric tons)
1954	210	4
1955	221	20
1956	155	33
1957	201	7
1958	273	22
1959	311	33
1960	412	31
1961	494	52
1962	497	20
1963	427	13
1964	424	50
1965	477	41
1966	356	53
1967	509	128
1968	369	91
1969	351	92
1970	362	78
1971	323	54
1972	434	57
1973	451	59
1974	399	31
1975	406	69

Aspects of and trends in the pelagic fishery have been discussed by Du Plessis (1959), Stander and Le Roux (1968), Baird and Geldenhuys (1973), Geldenhuys (1973), Newman *et al.* (1977) and Centurier-Harris and Crawford (1974b). The biology of pilchard, maasbanker and anchovy was investigated by Davies (1957), Robinson (1966), Pollock (1970), Baird (1970) and Geldenhuys (*op. cit.*).

Although mackerel contributed considerably to the annual yield, little attention was previously given to the species, and research was therefore initiated in an attempt to provide some understanding of the stocks. This report discusses the geographical distribution of the catches, their seasonal trends and their length and age composition.

DATA COLLECTION

Information on catch position was obtained from the returns of individual fishing boats. Between 1954 and 1967, the commercial catches were sampled for length, whole mass, sexual maturity and stomach contents at three field stations situated at Gans Bay, Hout Bay and Saldanha Bay. From 1968, age material was also collected. Unless otherwise stated, the lengths quoted are the standard body lengths, i.e. the distance between the tip of the snout and the posterior end of the caudal peduncle. All catch figures are in metric tons.

The age composition of the mackerel catches for the period 1968–1973 was determined from otolith readings. The numbers of otoliths used were:

1968	1969	1970	1971	1972	1973
381	411	191	400	431	561

RESULTS

Catch and size distribution

The annual and monthly distributions of the catches given in this report are based on the updated figures given by Crawford *et al.* (1978).

From 1954, when the mackerel catch was 4 044 tons (1,9 per cent of the total pelagic catch), to 1966 (53 426 tons, 14,9 per cent) the catch increased steadily. The largest catch was made in 1967 (128 219 tons, 25,1 per cent) but since then it has declined steadily and from 1971 to 1975 averaged approximately 50 000 tons (Table I). From 1967, the mackerel catch has been second only to the anchovy in importance in terms of mass during most years.

Mackerel catches before 1968 were generally made in the fishing area indicated in Figure 1. In the winter of 1968, however, with the aid of aerial fish spotting which had recently been introduced, mackerel shoals were sighted further off shore, north-west of Cape Columbine (Fig. 2). Exploitation of this deep-water resource was enhanced by the charter of a specialized large purse-seiner from Norway, the conversion of a local side trawler for purse-seining and by increasing the depth of the large-meshed nets of the existing West Coast fleet.

The catches were not evenly distributed over the fishing grounds, so in order to delineate the areas of high mackerel abundance, Centurier-Harris and Crawford (1974a) divided the total pelagic fishing grounds into 28 sections. In this report, these have been condensed into the eight areas shown in Figure 3. The mackerel yield per area between the years 1964 and 1972 (Table II) shows that the largest proportion of the annual catch was made between latitudes 32°20′S and 33°40′S (areas 2 and 3). Mackerel therefore appear to have been more available to the fishery in this area than elsewhere on the fishing grounds. Areas 1 and 4 also yielded considerable catches during some years. The catches in other areas were infrequent and constituted a very small proportion of the total annual catch.

Table III shows the mackerel catch per month for the period 1964–1973. Catches were made throughout the pelagic fishing season but fluctuated widely from month to month and also between the same months of different seasons. It appears, however, that prior to 1968 and to a lesser extent after 1971, the majority of the catches were made during the first five months of the year. From 1968 to 1971, catches during June and July also yielded a substantial proportion of the annual catch. This difference in pattern can be attributed to the appearance in the 1968 catches of off-shore mackerel which were caught mainly during the period June to September. In contrast; the catches during other months consisted of small to medium-sized, sexually immature fish.

The contribution of the off-shore component towards the total annual mackerel catch is reflected in Table IV. The largest catch of off-shore mackerel was made in 1970 (60 549 tons), constituting 77,7 per cent of the total mackerel catch and 16,7 per cent of the total pelagic catch. Since then the off-shore mackerel catch has declined steadily, only 962 tons being landed in 1975.

The fishing effort expended on the mackerel stocks is influenced by the availability of pilchard and anchovy at certain times of the year. Pilchard in the southern part of the pelagic fishing grounds, i.e. east of Cape Point during

Table II: Proportion of mackerel caught in each fishing area, 1964 – 1972

Year	Percentage							Mackerel catch (metric tons)
	Area 1	Area 2	Area 3	Area 4	Area 5	Area 6	Area 7	
1964	3,2	23,8	56,9	13,4	1,0	1,6	0	50 024
1965	6,4	77,1	14,6	1,9	0	0	0	41 426
1966	23,1	61,0	14,3	1,4	0,1	0,1	0	53 426
1967	2,6	5,6	63,1	21,9	5,3	1,5	0	128 219
1968	13,1	32,8	61,6	9,7	0,6	2,1	0,1	91 038
1969	8,3	47,8	28,4	14,5	0,3	0,7	0	91 702
1970	4,8	55,3	33,5	6,3	0	0	0,1	77 939
1971	15,5	56,8	13,7	4,4	1,2	8,2	0,2	54 230
1972	7,0	69,4	2,1	4,6	7,3	10,9	0	56 663
Mean	8,4	41,2	35,1	10,8	2,1	2,4	0,1	

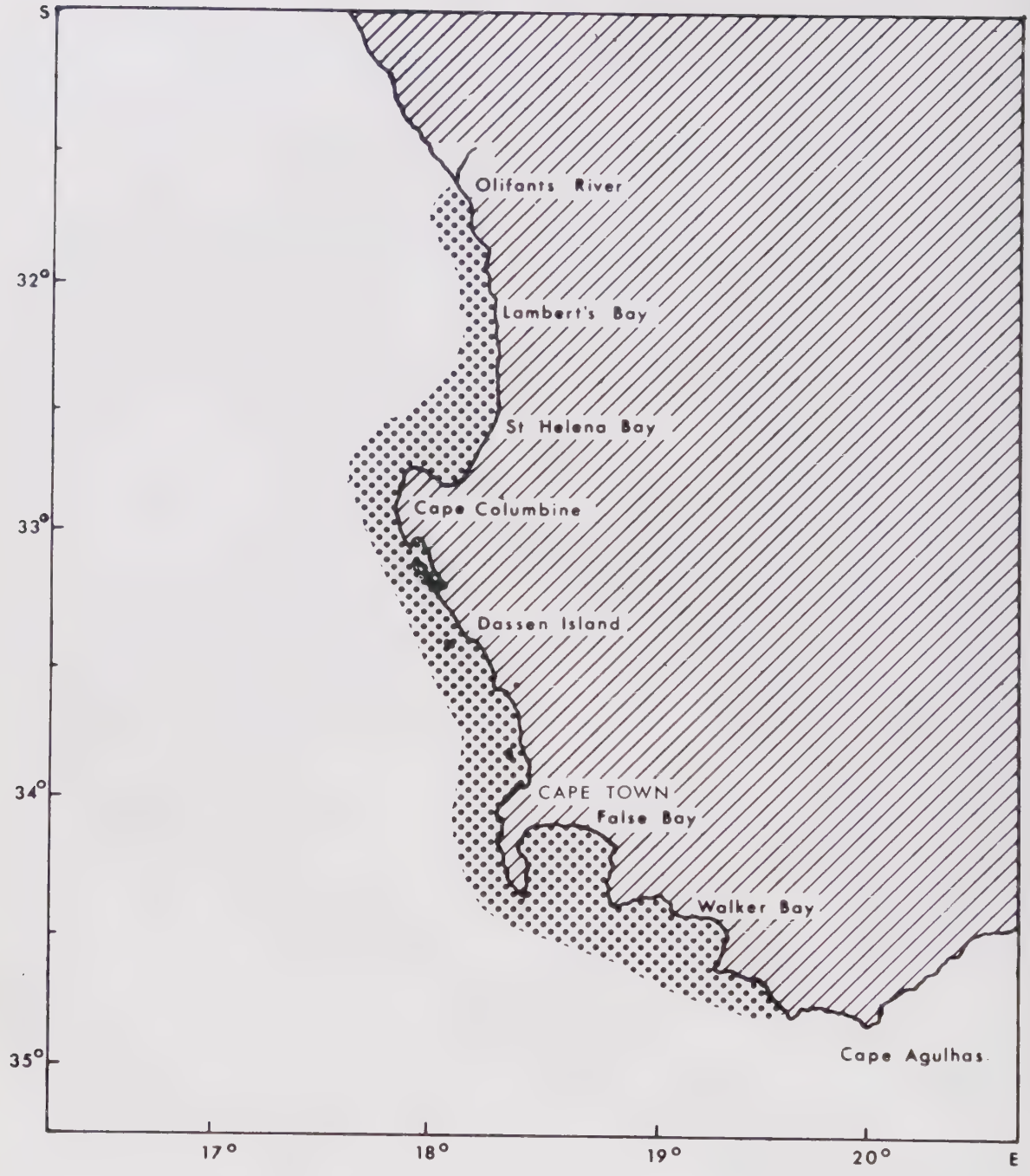

Fig. 1: Mackerel fishing grounds before 1968

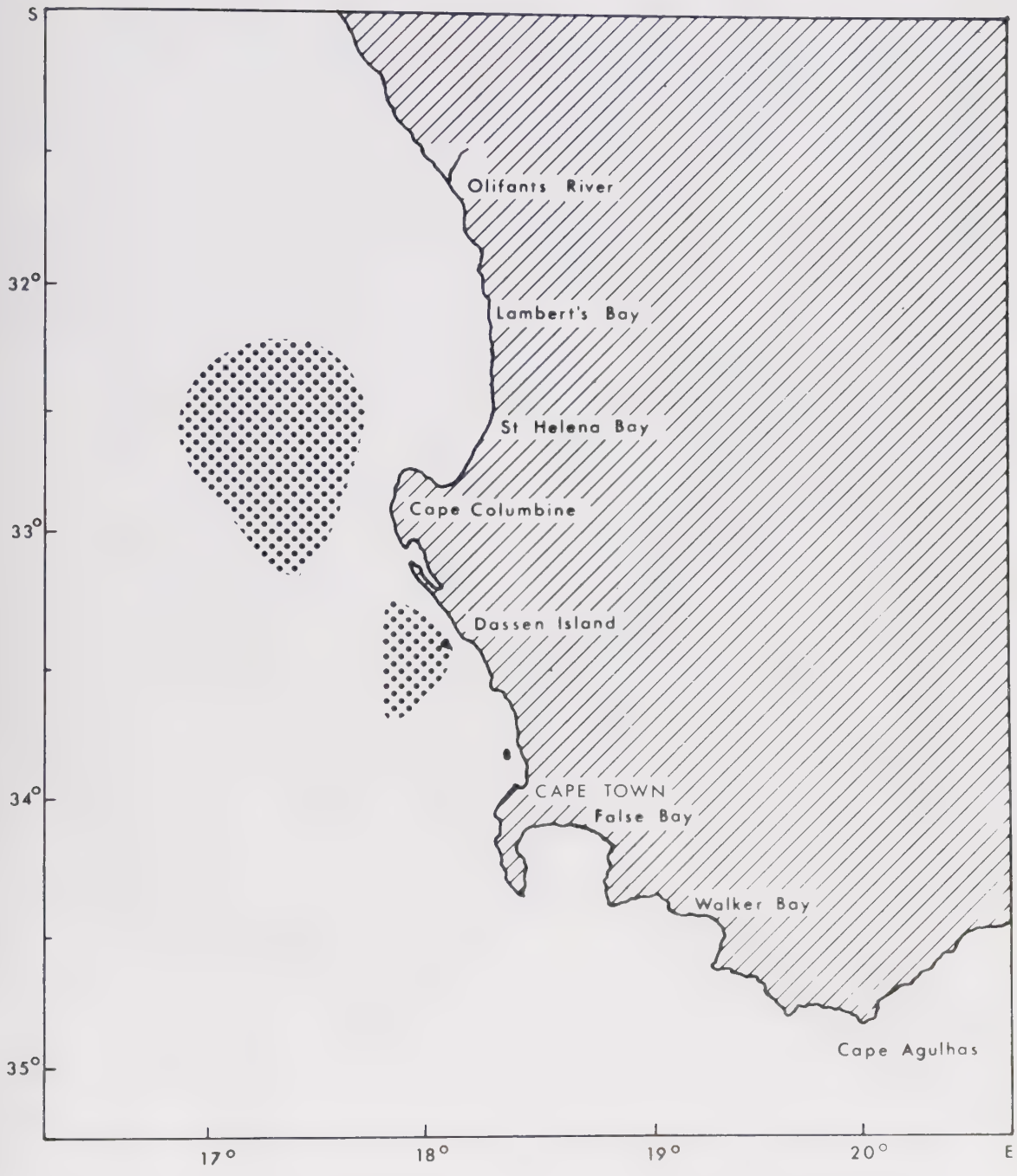

Fig. 2: Fishing grounds for large, off-shore mackerel, 1968 – 1973

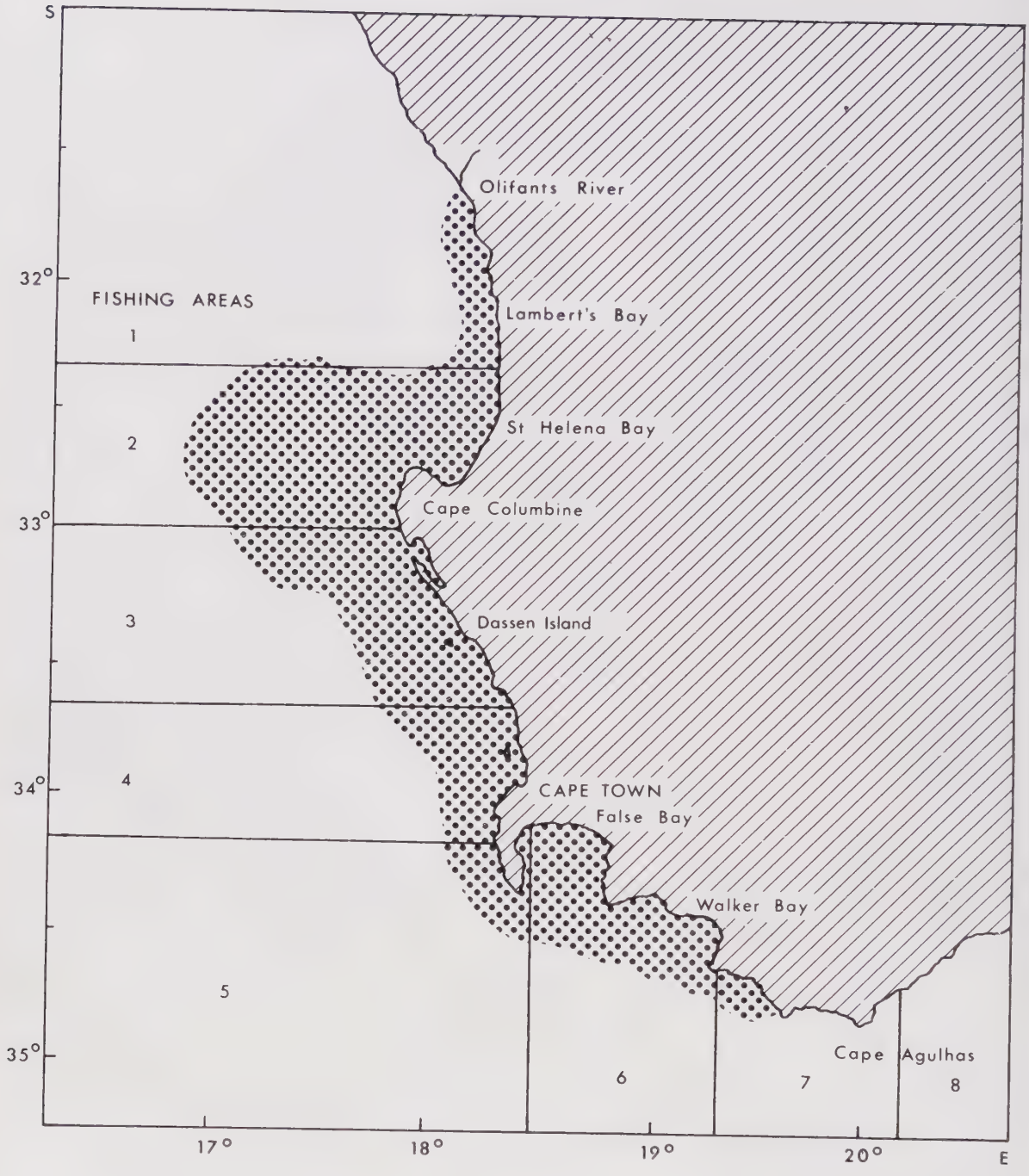

Fig. 3: Division of the pelagic fishing grounds into eight areas (the shaded area represents the mackerel catch locations, 1964 – 1972)

Table III: Total pelagic catch, total mackerel catch and off-shore mackerel catch per month, 1964 – 1973

Year		Catch per month (thousands of metric tons)											
		J	F	M	A	M	J	J	A	S	O	N	D
1964	Pc	61,7	56,8	67,4	43,0	53,4	37,4	35,0	3,9	21,5	28,0	19,0	4,6
	Mc	0,5	8,2	15,1	12,4	12,0	0	1,6	0	0	0	0	0,1
	Omc	0	0	0	0	0	0	0	0	0	0	0	0
1965	Pc	35,2	53,8	102,2	66,5	29,1	61,7	53,7	4,9	29,3	26,9	14,1	4,2
	Mc	3,9	9,5	11,6	16,4	0,1	0	0	0	0	0	0	0
	Omc	0	0	0	0	0	0	0	0	0	0	0	0
1966	Pc	19,3	30,5	54,4	53,6	55,0	72,4	22,3	31,8	18,7			
	Mc	2,5	4,3	14,0	19,7	12,9	0,1	0	0	0	Closed season		
	Omc	0	0	0	0	0	0	0	0	0			
1967	Pc	35,8	64,2	119,0	51,8	65,9	35,4	54,3	51,5	31,4			
	Mc	0,7	7,5	91,8	19,5	8,7	0	0	0,1	0	Closed season		
	Omc	0	0	0	0	0	0	0	0	0			
1968	Pc	52,5	50,4	38,6	38,3	54,7	35,6	62,1	14,2	22,5			
	Mc	19,6	1,6	1,2	2,7	6,6	9,3	49,3	0,8	0	Closed season		
	Omc	0	0	0	0	0	0	0	0	0			
1969	Pc	61,7	37,6	19,7	39,4	58,9	67,5	58,9	7,5				
	Mc	13,6	2,6	0,2	1,0	13,0	16,9	41,5	2,9	Closed season			
	Omc	0	0	0	0	0	14,6	38,5	2,7				
1970	Pc	37,0	32,5	49,8	71,3	44,9	22,9	79,2	24,5				
	Mc	0,2	0	1,6	0	0	6,7	69,4	0	Closed season			
	Omc	0	0	0	0	0	4,2	56,3	0				
1971	Pc	42,1	23,8	58,9	41,2	26,3	37,8	75,6	11,5	5,5			
	Mc	0	0,8	16,6	3,8	1,1	1,0	20,7	4,8	5,5	Closed season		
	Omc	0	0	0	0	0	0,3	20,3	2,7	2,7			
1972	Pc	44,2	46,5	55,3	45,0	129,2	36,4	64,4	14,0				
	Mc	9,3	8,6	27,5	2,5	0,7	0	8,0	0	Closed season			
	Omc	0	0	0	0	0	0	7,7	0				
1973	Pc	64,5	72,8	63,2	63,5	153,9	27,0	0	6,4				
	Mc	0,2	9,7	38,3	0,3	3,9	0,1	0	6,4	Closed season			
	Omc	0	0	0	0	0	0	0	6,4				

Pc = total pelagic catch
Mc = total mackerel catch, including off-shore mackerel
Omc = off-shore mackerel catch only

January and February, attract a large proportion of the fishing effort (Baird 1973) and from April onwards, effort is directed mainly towards anchovy (Baird and Geldenhuys 1973). It is, thus, only towards the end of the fishing season when the off-shore mackerel enter the grounds, that a considerable amount of fishing effort is expended on this species. It then constitutes a large proportion of the pelagic catch during the later months (Table III).

Table IV: Contribution of off-shore mackerel to the total mackerel catch, 1967 – 1975

Year	Total mackerel catch	Off-shore mackerel catch	Percentage of total mackerel catch
1967	128 219	0	0
1968	91 038	25 300	27,8
1969	91 702	55 787	60,8
1970	77 939	60 549	77,7
1971	54 230	26 095	48,1
1972	56 663	7 712	13,6
1973	58 835	6 415	10,9
1974	30 665	0	0
1975	69 344	962	1,4

Table V: Percentage age composition of mackerel catch, 1968 – 1973

Year	Age class								
	O+	I+	II+	III+	IV+	V+	VI+	VII+	VIII+
1968	6,0	40,1	39,6	6,9	6,3	1,1			
1969	19,0	28,6	33,2	11,3	5,1	2,1	0,8		
1970	1,8			12,6	50,0	21,9	11,3	2,1	0,3
1971	29,8	15,5	29,1	10,8	7,6	3,8	2,3	0,8	0,1
1972	7,1	54,9	28,7	6,7	1,0	0,8	0,4	0,2	0,1
1973		11,5	65,4	13,8	8,1	1,2			

Composition of mackerel catches

The annual length frequency distribution of mackerel caught from 1954 to 1973 is illustrated in Figure 4. It is evident that variation between years was great. Annual catches consisted either of a uni-modal group of fish with a relatively limited length range (1957, 1958, 1959, 1962) or of bi-modal or multi-modal groups of fish covering a broader length range (1954, 1955, 1956, 1960, 1961, 1963 to 1973).

Age composition data (Table V) show that the catch for the period 1968 to 1973 consisted of several age groups each year. Dominant age classes were I+ and II+ in 1968, 1969 and 1972, IV+ in 1970, 0+ and II+ in 1971 and II+ in 1973. The importance of the older age classes in the landings is reflected by the mass distribution of the catches (Table VI).

From an analysis of the length frequency and the age composition of the mackerel catches for the period 1968 to 1973, coupled with a knowledge of the positions and time of the year at which these catches were made, a clear picture of mackerel availability has emerged. Two groups of mackerel could be identified, namely an inshore and an off-shore group.

Inshore mackerel – These were predominantly small and medium sized. The small mackerel varied in length from 10 cm to 25 cm, were sexually immature and were generally less than one year old. They were available to fishermen throughout the fishing season, not always shoaling separately but often found in association with the round herring *Etrumeus teres*.

Medium-sized mackerel ranged in length from 25 cm to 45 cm and were between one and four years old with the modal age distribution at I+ and II+. The majority of these fish were also immature except for a small percentage in the higher age classes (III+ and IV+) during winter. Catches of medium-sized mackerel were pure and were usually made between St Helena Bay and Dassen Island.

Inshore mackerel formed the bulk of the annual mackerel yield from 1954 to 1975 with the exception of 1969, 1970 and possibly 1956, 1957 and 1965. With the exception of 1970 and 1971, when the 0+ fish contributed 100 per cent and 39 per cent of the inshore catch respectively, the I+ and II+ year classes predominated. In 1971, II+ fish were numerically sub-dominant to the 0+ (Table VII), but contributed a much higher percentage in terms of mass to that year's inshore mackerel catch (Table VIII).

Off-shore mackerel – These can be distinguished

Table VI: Percentage mass distribution per age class of total mackerel catch, 1968 – 1973

Year	Age class								
	O+	I+	II+	III+	IV+	V+	VI+	VII+	VIII+
1968	1,3	20,9	40,4	14,4	19,2	3,8			
1969	3,1	14,7	33,5	23,2	15,2	7,1	3,0		
1970	0,1			8,4	48,6	24,2	14,3	3,9	0,5
1971	4,2	6,9	25,5	19,3	19,9	11,7	7,8	4,1	0,6
1972	1,4	35,0	35,9	17,5	3,7	3,3	1,9	1,0	0,3
1973		4,6	51,2	22,1	18,8	3,3			

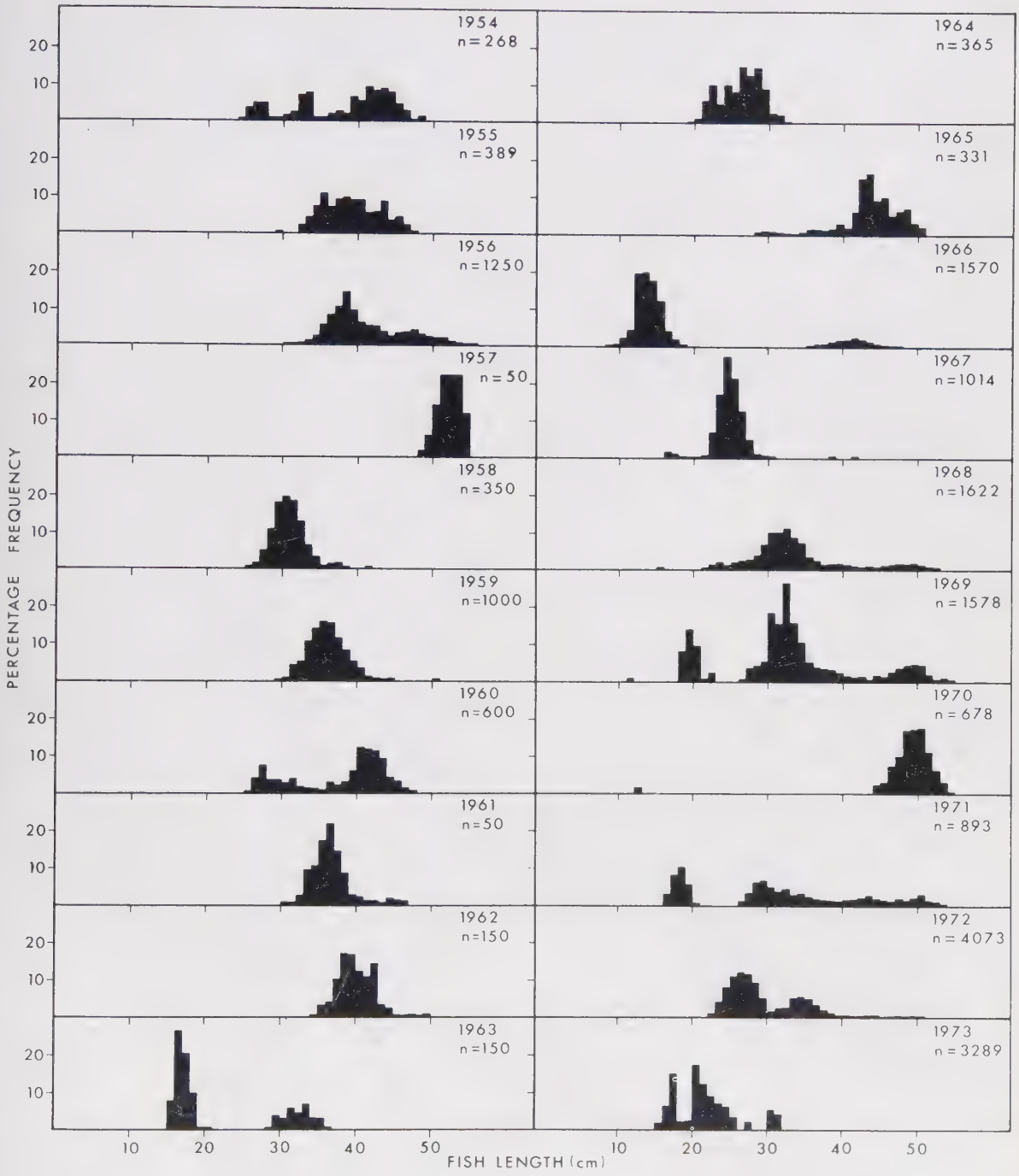

Fig. 4: Length frequency distribution of the catch, 1954 – 1973 (n is the number of fish measured)

Table VII: Percentage age composition of inshore mackerel catch, 1968 – 1973

Year	Age class				
	O+	I+	II+	III+	IV+
1968	6,9	50,6	42,2	0,4	
1969	23,1	34,6	36,9	5,4	
1970	100,0				
1971	38,6	20,0	30,2	7,1	4,1
1972	7,8	58,8	27,5	5,4	0,5
1973		16,6	76,9	6,5	

from inshore mackerel on the basis of position and time of catch, age composition and sexual maturity. Off-shore mackerel appeared in the fishing grounds during winter each year from 1968 to 1973. They did not appear in 1974, but a small catch was again made during 1975. Catches were usually made in the areas indicated on Figure 2. Age composition data (Table IX) show that the majority were III+ and older and, as mackerel attain sexual maturity in their third year of life (Baird 1974), most had already attained sexual maturity. All observed gonads were in advanced stages of development and a few females were spent.

Table VIII: Percentage mass distribution per age class of inshore mackerel catch, 1968 – 1973

Year	Age class				
	O+	I+	II+	III+	IV+
1968	1,6	37,0	60,0	1,4	
1969	5,4	25,5	53,1	15,9	
1970	100,0				
1971	8,6	13,9	41,1	19,7	16,6
1972	1,8	42,1	38,5	15,4	2,1
1973		8,6	77,9	13,4	

The occurrence of off-shore mackerel can be linked with spawning. Concentrations of eggs were found off the Cape west coast between Lambert's Bay in the north and Dassen Island in the south from June to September 1973. This period has since been defined as the spawning season of the mackerel (Baird 1974), and thus the off-shore component of the mackerel stock can be considered as the adult, spawning population.

Sex ratio

Annual ratios of males to females in the commercial catches for the years 1966–1973, as well as the mean ratio over the whole period, are shown in Table X. With the exception of 1972, the ratios were close to 1:1 with the females seeming to have a slight predominance over males in most years. The mean ratio over the entire period (1:1,14) was, however, nearly unity and could be accepted as such for practical purposes. The ratio of males to females per 1–cm size class for the period 1966–1971 is shown in Table XI. The predominance of one sex over the other varies from size class to size class. However, in the larger size classes, females were consistently more common than males, their predominance being of the order of 13,5 per cent between the lengths of 46 cm and 55 cm (age classes IV+ and higher). The sex-ratio data were consequently subjected to a statistical analysis which showed that the proportion of males in fact decreases linearly with increasing fish size with a probability $P < 0,05$ (Snedecor and Cochran 1967).

The males of many fish species mature earlier and die earlier than females, thus accounting for the slight predominance of females in the larger size groups (Nikolskii 1969). Although not evident from the growth curves of males and females or from length-at-maturity (Baird 1977), the sex ratios (Table IX) suggest that this may, in fact, be the case for mackerel.

Table IX: Percentage age composition of off-shore mackerel catch, 1968 – 1973

Year	Age class								
	O+	I+	II+	III+	IV+	V+	VI+	VII+	VIII+
1968				36,6	54,8	8,6			
1969		0,1	12,7	35,2	36,6	12,3	3,0		
1970				12,6	50,3	22,9	11,9	2,2	0,3
1971		6,5	19,9	21,9	17,4	17,2	11,0	4,5	2,0
1972			22,7	40,7	21,0	12,6	3,0		
1973		2,3	40,5	29,2	24,6	3,3			

Table X: Sex ratio of commercial catch, 1966 – 1973

Year	Ratio			Number of fish	
	Males	:	Females	Males	Females
1966	1	:	0,91	351	319
1967	1	:	1,09	471	515
1968	1	:	1,01	823	831
1969	1	:	1,30	667	867
1970	1	:	0,99	331	329
1971	1	:	1,21	175	211
1972	1	:	2,23	148	330
1973	1	:	1,08	168	182
1966–1973	1	:	1,14	3 134	3 584

DISCUSSION

From the results presented, two phases can be distinguished in the life history of mackerel. Both these phases, inshore and off shore, are commercially exploited. The availability of off-shore mackerel during winter appears to be affected by prevailing environmental conditions. During winter, the south-east trades are at a minimum while the frequency of north-westerly winds is at a peak, upwelling is virtually non-existent inshore and the Benguela Current is weak, at times merely a shallow drift moving in the direction of the prevailing wind. The on-shore current is most pronounced during winter and, consequently, relatively warm water (14–15°C) makes its appearance close inshore during this period (Shannon 1976). Mackerel were only caught during those periods when there was an easterly component of movement of the mixed surface layer, i.e. during times of minimum upwelling, when oceanic surface water was pushed into the area. No mackerel were caught during the months when the surface drift was a clearly defined flow in a northerly to north-westerly direction.

The off-shore/inshore migration of *Scomber japonicus* has also been observed in other parts of the world and that of *S. scombrus* in the North Atlantic. Gagliardi and Cousseau (1970) have reported on the inshore appearance of *S. japonicus marplatensis* off the east coast of Argentina between December and February each year. Kwei (1970) has observed the yearly inshore migration of large mackerel from deeper off-shore waters from June to December off the coast of Ghana. In both these studies, the inshore appearance of mackerel was closely linked with spawning.

Table XI: Mean sex ratio (per 1-cm size class) in commercial catch, 1966 – 1971

Size class (cm)	Ratio			Number of fish
	Males	:	Females	
27,0–27,9	1	:	1,08	199
28,0–28,9	1	:	0,96	143
29,0–29,9	1	:	1,08	129
30,0–30,9	1	:	0,87	202
31,0–31,9	1	:	1,01	295
32,0–32,9	1	:	0,99	316
33,0–33,9	1	:	0,97	326
34,0–34,9	1	:	1,02	249
35,0–35,9	1	:	1,21	217
36,0–36,9	1	:	0,92	138
37,0–37,9	1	:	1,41	142
38,0–38,9	1	:	1,49	142
39,0–39,9	1	:	1,11	177
40,0–40,9	1	:	1,01	183
41,0–41,9	1	:	0,99	175
42,0–42,9	1	:	0,88	184
43,0–43,9	1	:	0,99	145
44,0–44,9	1	:	1,09	109
45,0–45,9	1	:	0,93	108
46,0–46,9	1	:	1,09	92
47,0–47,9	1	:	1,40	139
48,0–48,9	1	:	1,01	171
49,0–49,9	1	:	1,08	221
50,0–50,9	1	:	1,32	234
51,0–51,9	1	:	1,20	233
52,0–52,9	1	:	2,27	124
53,0–53,9	1	:	0,92	67
54,0–54,9	1	:	1,47	42
55,0–55,9	1	:	2,00	9

Atlantic mackerel (*S. scombrus*) are seasonal migrants to Newfoundland waters. They appear in abundance in July and disappear in October and November (Moores *et al.* 1975). Sette (1950) has reported on the migration of adult *S. scombrus* along the east coast of North America. He found them in commercial quantities inshore only from April to July, but then an off-shore migration resulted in their being seldom seen or caught. *S. scombrus* also appear in inshore waters off the south-west coast of England during summer, but disappear from the fishing grounds in the autumn (Bolster 1971).

The mackerel in the Western Cape waters thus exhibit a migration similar to that of scombrids in other parts of the world. In addition, the majority of off-shore mackerel had gonads in advanced stages of maturity (active to ripe), and it is thus concluded that the appearance of off-shore mackerel in the inshore fishing grounds is associated with spawning. Reasons for their disappearance further south, in the vicinity of Dassen Island, are not known. Also, the seaward extent of the adult mackerel stock has not been delimited.

The two components of the mackerel stock are clearly interdependent. Off-shore mackerel depend on recruitment of younger, inshore mackerel to maintain their stock size and viability as an adult population. The rate of recruitment of inshore to off-shore mackerel would be subject to the intensity of fishing on the inshore stock, a factor which is not known. It is, therefore, at present impossible to estimate the quantitative effect of inshore mackerel fishing on the off-shore component.

The decline in the off-shore mackerel catch since 1970 can be ascribed either to reduced availability (possibly due to environmental changes) or to a decrease in abundance (possibly as a result of heavy fishing pressure on the inshore component). Templeman (1966), for example, has shown that abundance of the Atlantic mackerel *S. scombrus* in Newfoundland waters has fluctuated in response to environmental conditions. In a pelagic species such as the mackerel where the vertical as well as the horizonal distribution affects the quantity caught, availability will have a much more pronounced effect on the catch than on that of non-pelagic and some other pelagic species.

ACKNOWLEDGEMENTS

I am grateful to Dr B. van D. de Jager, Director of Sea Fisheries, who made this study possible. I wish to thank him, Prof. C. A. du Toit (Zoological Institute, University of Stellenbosch), Dr G. G. Newman and Messrs D. E. Pollock, R. J. M. Crawford, O. M. Centurier-Harris and N. D. Geldenhuys of the Sea Fisheries Branch for many helpful suggestions. A special word of thanks is due to Messrs G. H. L. Wingate, G. B. Tong and F. Kriel who were responsible for most of the collection and preliminary analysis of the data.

The assistance of Prof. N. F. Laubscher and Dr A. G. de Wet, Department of Mathematical Statistics, University of Port Elizabeth, in the statistical treatment of the data is gratefully acknowledged.

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This report is based on a section of a dissertation submitted in June 1974 as part requirement for the degree of Doctor of Philosophy at the University of Stellenbosch.

Fish. Bull. S. Afr. 10:62–68
1978

FOOD OF THE MACKEREL *SCOMBER JAPONICUS* FROM WESTERN CAPE WATERS

D. BAIRD

Apart from studies by De Jager *et al.* (1963) and Penrith (1963) on four tuna species, little is known about the diet of South African scombrid fishes.

The mackerel *Scomber japonicus* Houttuyn occurs in commercially exploitable quantities along the Cape west coast from Lambert's Bay in the north to Cape Agulhas in the south. Mackerel also occur along the Eastern Cape Coast and may even penetrate as far east as Natal, but are of little commercial importance in these areas. Although the annual catches fluctuate widely from year to year, the species is nevertheless a significant contributor to pelagic catches (Baird 1975).

In view of the commercial importance of mackerel and the lack of information on its feeding habits, a study of stomach contents collected from a wide size range of fish caught off the Western Cape during the fishing seasons 1969–1971 was made.

MATERIAL AND METHODS

There are several reliable methods of evaluating the food components of fish stomachs. Most workers have based their studies on stomach contents, but a few have examined the contents of the entire alimentary tract. Identification of organisms in the stomach is usually more satisfactory, because digestion is less advanced and, thus, only the stomach contents were examined in this study. Stomachs for analysis were obtained from commercial catches made between Lambert's Bay and Cape Agulhas.

During the analysis of a fish sample, the state of repletion of the stomach of each individual fish was given an index of full, half-full, nearly empty or empty. The entire stomach was carefully removed, weighed to the nearest 0,1 g and labelled for future study. When the contents were examined, food items were identified to species wherever possible. Zooplankton organisms in advanced stages of digestion which could not be identified with any degree of certainty were lumped under "unidentifiable zooplankton". Provision was also made for digested fish remains.

The stomach contents of 257 mackerel were collected during the period January 1969 – September 1971, excluding the closed pelagic season between September and December each year. Table I reflects the number of fish in each centimetre standard length group examined for stomach contents.

Differences were observed in the diet of mackerel of different size classes and thus, to facilitate the interpretation of the feeding data, the fish were categorized into three size groups. These were as follows:

small mackerel, 25 cm and less;
medium-sized mackerel, 26–45 cm long;
large mackerel, 46 cm and longer.

The number of fish examined in each size category is shown in Table II.

Small mackerel were sampled only during January and March, medium-sized fish only during autumn and winter and large mackerel mainly during winter (see Table I). Consequently, the seasonal variability in the diet of the mackerel could not be investigated, and also insufficient material precluded a study of diurnal variation in feeding.

In some feeding studies, authors have merely listed food organisms found in the stomach. However, such a presentation of results does not give an indication of the relative importance of each type of organism. Different methods have therefore been devised for the analysis of feeding data and some of these are briefly outlined below.

(a) The frequency-of-occurrence method: The number of fish in which each food item occurs is listed as a percentage of the total number of fish examined. The number of occurrences of all items are then added and expressed as a percentage to show the composition of the diet.

(b) The numerical method: Each individual food item is counted and expressed as a percentage of the total number of all organisms found in all fish examined.

(c) The volume and mass method: The displacement volume or the mass of each food item is expressed as the percentage of the total volume or mass of the stomach content. According to

Table I: Length frequency distribution of mackerel examined for food

Length class (cm)	Month									Total
	J	F	M	A	M	J	J	A	S	
10,0–10,9	1									1
11,0–11,9	2									2
12,0–12,9	1									1
13,0–13,9			1							1
14,0–14,9										0
15,0–15,9										0
16,0–16,9										0
17,0–17,9										0
18,0–18,9			1							1
19,0–19,9			2							2
20,0–20,9			5							5
21,0–21,9			2							2
22,0–22,9										0
23,0–23,9			1							1
24,0–24,9										0
25,0–25,9										0
26,0–26,9										0
27,0–27,9										0
28,0–28,9		3								3
29,0–29,9		3								3
30,0–30,9		2					3	1		6
31,0–31,9										0
32,0–32,9			2							2
33,0–33,9		1	1		1		2			5
34,0–34,9		1	2					2	1	6
35,0–35,9			2		1		1			4
36,0–36,9			4		3			1		8
37,0–37,9			2		5		2	2		11
38,0–38,9			3		1		1	2	1	8
39,0–39,9			2		3		2	4	2	13
40,0–40,9			2		1		3	8	1	15
41,0–41,9					1			7		8
42,0–42,9			5				1		1	7
43,0–43,9			7					2	1	10
44,0–44,9			5				1	3	2	11
45,0–45,9			3			1	1		6	11
46,0–46,9			1			1	4	1	1	8
47,0–47,9			2			1	6			9
48,0–48,9						2	11	1		14
49,0–49,9						1	15			16
50,0–50,9						4	14	1		19
51,0–51,9						10	10			20
52,0–52,9						3	5			8
53,0–53,9						1	10			11
54,0–54,9						1	2			3
55,0–55,9						1				1
56,0–56,9							1			1
Total	4	10	55	0	16	26	95	35	16	257

Dragovich (1969), this method reliably depicts the relative importance of various food items. However, the method is mostly used as a supplement to another (Dragovich *op. cit.*, Hynes 1950). (d) The points method: This method was developed by Swynnerton and Worthington (1940) and later slightly modified by Frost (1943). It has the advantage of giving approximately quantitative as well as qualitative results, without the need for detailed counts or weighings. It is rapid and easy, does not require special apparatus for measurements, is not influenced by the frequent occurrence of small organisms in small numbers or by the occurrence of heavier bodies such as fish and it does not involve trying to count large numbers of small or broken organisms. The points method was therefore used in this study.

According to the points system of Swynnerton

Table II: Number of fish examined for food in each mackerel size category

Length category	Number
Small (< 25 cm)	16
Medium (26 cm–45 cm)	131
Large (> 46 cm)	110

and Worthington (1940), the organisms of each food category were either roughly counted or their masses macroscopically assessed. Due consideration was given both to the size of organisms and to their abundance, i.e. one large organism counted as much as a number of small ones. Each food item was then allotted a number of points according to its relative volume and numerical frequency. Frost (1943) stated that such an evaluation was essentially an estimate of bulk and that the points represented absolute values and not relative ones. Therefore, the fullness of the stomach had to be taken into account. Furthermore, Hynes (1950) suggested that it was better to allot points to the total content of the stomach in the first instance and then to subdivide the allotted number of points to the various food items. A full mackerel stomach was subsequently allotted 10 points, a half-full stomach 5 points and a nearly empty stomach 1 point.

The following example explains the method. A full stomach of a medium-sized mackerel was allotted 10 points. It contained two lantern-fish (mass 10 g), about 200 euphausiids (mass 8 g), a few amphipods and some unidentifiable, digested fish remains. Lanternfish and euphausiids constituted the bulk of the contents and were allotted 4 points each. The unidentifiable fish remains were given 1½ points and, although the amphipods outnumbered the fish, they were allotted ½ point as they constituted only a minor proportion of the contents. All stomachs were examined on this basis.

The total number of points for each food item for each of the three mackerel size categories were added and converted into a percentage composition of the food for all fish examined. The difficulty of maintaining a standard in points allotment was largely overcome by repeating the analysis of the contents of a number of individual stomachs with a time lapse between the examinations. A comparison of the composition of the same contents obtained repeatedly indicated that the allottment of points to the various food items became more consistent as the examiner gained experience with the method.

The composition of the stomach contents was also determined by the frequency-of-occurrence method, but it was found that undue emphasis was placed on the presence of large numbers of zooplankton organisms and that the importance of fish as food of the mackerel was underestimated. Results of this method are therefore not presented here.

RESULTS

The food organisms identified in the stomachs of the different size categories of mackerel, classified to species where possible, are listed in Table III. The percentage composition of the various food items, as determined by the points method for each of the three size categories, is also shown. Figure 1 summarizes the food intake of the different size classes of mackerel. It is evident that differences exist in the composition of the diet of these three size categories.

Table III shows that 30 species of fish and intervertebrates were identified in the stomachs of all the mackerel examined. All species were typically planktonic and mesopelagic, none being bottom fauna. Four species of fish, twenty-one species of crustacean, two species of mollusc, one tunicate and one chaetognath were identified. In terms of number and volume, the bulk of intervertebrates were euphausiids and amphipods. Other invertebrate species occurred less frequently and in smaller numbers.

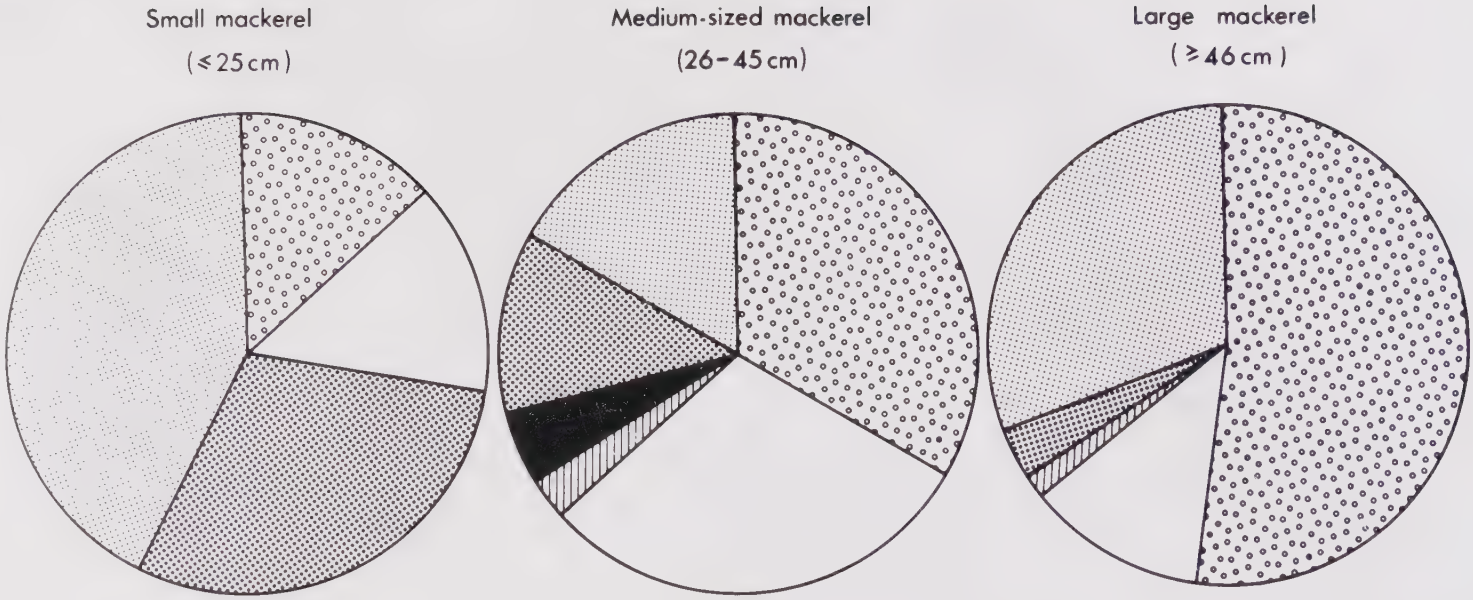
DISCUSSION

In small mackerel (25 cm and shorter), fish constituted 13,5 per cent of the diet and ranked third in importance. The ingested fish varied in total length between 2,5 cm and 3,5 cm but none could be positively identified owing to the advanced state of digestion. Consequently, they were classified as unidentifiable fish remains.

The fish component increased to 33,5 per cent in the diet of medium-sized mackerel. Ingested fish ranged from 4,6 cm to 10,4 cm in total

Table III: Percentage composition of the food per mackerel size category (points method)

Food item	Mackerel size category		
	Small	Medium	Large
TELEOSTEI	13,5	33,5	52,5
Lampanyctodes hectoris	–	22,6	44,4
Protomyctophum spp.	–	–	0,7
Engraulis capensis	–	2,3	–
Etrumeus teres	–	1,3	0,6
Unidentifiable fish remains	13,5	7,3	6,8
EUPHAUSIACEA	42,6	16,5	30,3
Euphausia lucens	+	+	+
Nyctiphanes capensis	+	+	+
Euphausiid furcilia	+	+	+
AMPHIPODA	30,0	12,2	3,6
Parathemisto gaudichaudi	+	+	+
Paramoera capensis	+	+	+
Other hyperiid spp.	+	+	+
Gammarid spp.	+	+	+
COPEPODA	0,2	4,7	8,1
Nannocalanus minor	+	+	–
Calanoides carinatus	+	+	+
Metridia lucens	+	+	–
Centropages brachiatus	+	+	+
Centropages spp.	–	–	+
Pleuromamma gracilis	+	+	–
Candacia bipinnata	–	+	–
Clausocalanus spp.	+	+	+
Sapphirina spp.	–	+	–
Oncaea spp.	–	+	
MYSIDACEA	–	0,01	–
Siriella jaltensis	–	+	–
DECAPODA	–	–	+
OTHER CRUSTACEA		1,2	0,7
Squilla armata	–	+	–
Zoea larvae	–	+	–
Megalopa larvae	–	+	+
Phyllosoma larvae		–	+
CHAETOGNATHA			
Sagitta spp.		0,8	–
TUNICATA			
Salpa fusiformis		0,9	–
COELENTERATA			
Medusae (pieces)	–	0,2	–
MOLLUSCA	–	–	0,01
Loligo spp. } juvenile	–	–	+
Sepia spp. } juvenile	–	–	+
UNIDENTIFIABLE ZOOPLANKTON	13,7	30,0	12,8



	Percentage		
	S	M	L
Fish	13,5	33,5	52,5
Euphausiids	42,6	16,5	30,3
Amphipods	30,0	12,2	3,6
Copepods	0,2	4,7	0,1
Other identified zooplankton	–	3,1	0,7
Unidentified zooplankton	13,7	30,0	12,8

Fig. 1: Major components of the mackerel diet

length. The bulk of this particular food group was the lantern-fish *Lampanyctodes hectoris*, which constituted 22,6 per cent of the diet of this mackerel size category. Other common pelagic species, such as anchovy *Engraulis capensis* and round herring *Etrumeus teres*, accounted for a very small percentage of the diet of medium-sized mackerel (see Table III).

In large mackerel (longer than 45 cm), fish constituted the bulk of the food. As was the case for medium-sized mackerel, *Lampanyctodes hectoris* was the most common species encountered, accounting for 44,4 per cent of the total. Other fish species were only rarely found.

It is evident from the results presented in Table III that zooplankton was the main constituent of the diet of small and medium-sized mackerel, constituting 86,5 per cent and 66,5 per cent respectively of the food. These percentages include unidentifiable zooplankton. The proportion of zooplankton organisms in the stomach contents decreased with increase in fish size. Zooplankton accounted for only 47,5 per cent of the food of large mackerel.

Although crustaceans predominated in the stomachs (21 species identified), the variation in species composition between size categories of mackerel was considerable. However, Table III and Figure 1 show that *Euphausia lucens, Nyctiphanes capensis* and euphausiid furcilia predominated in the zooplankton component of each size group. Collectively they constituted 42,6, 16,5 and 30,3 per cent of the stomach contents of each of the three size categories respectively. The relatively low euphausiid percentage (16,5) for medium-sized mackerel was probably due to the inclusion of digested euphausiids in the "unidentifiable zooplankton" category which had a relatively high value of 30,0 per cent.

Amphipods ranked next in order of importance. They formed a major proportion of the diet of small mackerel (30,0 per cent) but a lesser proportion (12,2 per cent and 3,6 per cent respectively) of the stomach content of medium-sized and large mackerel. Copepods, other crustaceans, tunicates, molluscs and chaetognaths occurred rarely and in small numbers in the stomachs of the fish examined.

The decreasing importance of crustaceans (particularly amphipods and euphausiids) and the increasing predation on lantern-fish (particularly *Lampanyctodes hectoris*) as the mackerel grows, are noteworthy and indicative of a change in its vertical distribution and feeding habit. Small mackerel feed on zooplankton in the surface layers, whereas older and larger fish feed on mesopelagic lantern-fish. It would seem that as mackerel grow older, they show an increasing tendency to feed at depths greater than those during their younger stages. However, a small degree of surface or near-surface feeding is indicated by the continued presence of zooplankton in the stomachs of medium-sized and large mackerel. The feeding pattern of large mackerel is apparently closely associated with the diurnal, vertical migration of the food organisms.

In the stomachs of medium-sized and large mackerel, either fish or zooplankton (mainly euphausiids) predominated. The number of stomachs containing mixtures of these two food groups was small and it is concluded that mackerel feed on either fish or zooplankton at a given time. This does not necessarily imply food selectivity, but it is most probably due to the availability of the different food organisms to mackerel at different times and depths.

Fry (1936) stated that the Pacific mackerel *Pneumatophorus diego* on the west coast of the United States of America feed on a variety of food items such as copepods, anchovy and squid. He noted that the mackerel occurring in those waters showed little discrimination in their feeding and that any animal matter was acceptable as food. He also noted that the Pacific mackerel fed on one variety of food at a time. It seems, therefore, that the feeding habits of the Pacific and the South African mackerel are comparable.

The diet of *Scomber japonicus* is similar to that of some tuna species also occurring in the South Atlantic in that the same type of organism is preyed upon. De Jager *et al.* (1963) examined the stomach contents of four tuna species, *Thunnus thynnus orientalis* (blue-fin), *T. alalunga* (long-fin), *T. albacares* (yellow-fin) and *T. obesus* (big-eye). The results showed that these species fed on a wide variety of organisms including euphausiids, amphipods and several species of fish. Lantern-fish was also listed as a food item, although its relative importance was not indicated. However, the specific prey species differ, tuna apparently preying upon a greater number of fish species than do mackerel.

Small mackerel are mainly zooplanktophagous. Other pelagic species, e.g. pilchard and anchovy, also feed on zooplankton, but to a lesser extent (King and Macleod 1976). However, larger organisms such as euphausiids and amphipods predominate in the diet of small mackerel whereas smaller zooplankters, mainly copepods, are eaten by the other two species.

A study of the gill raker structure of mackerel should also reflect the changing preference for

different size prey organisms as the fish grows, and clarify the mechanism of food capture.

ACKNOWLEDGEMENTS

I wish to thank the Director of Sea Fisheries, Dr B. van D. de Jager, and Prof. C. A. du Toit, Zoological Institute, University of Stellenbosch, for their encouragement and advice. The assistance of Mr G. H. L. Wingate during this study is gratefully acknowledged.

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This report is based on a section of a dissertation submitted in June 1974 as part requirement for the degree of Doctor of Philosophy at the University of Stellenbosch.

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1978

REVISION OF SPECIES AND AGE COMPOSITION OF LANDINGS IN THE SOUTH AFRICAN PURSE-SEINE FISHERY, 1950 TO 1976

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G. H. L. WINGATE and B. D. KRIEDEMANN

Catch figures previously published for the South African purse-seine fishery in the Western Cape have been based upon factory estimates of the species composition of the catches off-loaded by their respective fishing units. Although the total mass (weight) of fish landed has always been recorded accurately, catches, especially since 1964, often comprised more than one species and were generally allocated *in toto* to the species most abundant in that landing. Juveniles of pilchard *Sardinops ocellata* and round herring *Etrumeus teres*, for example, frequently occurred in mixed catches in which anchovy *Engraulis capensis* was dominant and were catalogued as anchovy. It was anticipated that this would significantly influence not only the catch figures of these three species and of two other commercially caught fish, horse mackerel (maasbanker) *Trachurus trachurus* and mackerel *Scomber japonicus*, but also the age compositions determined from them. A second factor expected to bias these estimates was the use of field-laboratory information on the length distribution of the landings without any account being taken of the catch weight represented by each sample. A sixth species, the lantern-fish *Lampanyctodes hectoris*, also contributes to the fishery, but no age determination technique for this fish has yet been developed.

Sampling has been undertaken, though not always concurrently, at five separate landing points: Lambert's Bay, St Helena Bay, Saldanha Bay, Hout Bay and Gans Bay. As may be seen from Figure 1, these sites cover the factories participating in the fishery in a reasonably representative manner. Details of species composition and length distribution of the catches from known localities were recorded, while otoliths and scales were removed for subsequent age determination.

All skippers were requested to report the positions of their catches and the tonnages off-loaded. Landings form the basis of their remuneration, so that skipper estimates of total catch were reliable, but the position was not always recorded and had, in some cases, to be inferred from that of sister vessels operating from the same home port.

Factories have been required by law to supply accurate monthly catch totals and have, in addition, kept records of the approximate species composition of the landings.

These three sources of information have now been combined to obtain corrected catch figures and length and age compositions for each species (Fig. 2). The purpose of this report is to document the methods employed for future reference and to present the revised estimates of the annual catch and age compositions.

WEIGHTING PROCEDURES

The Western Cape purse-seine fishery was initiated in 1943, but no accurate records of performance are available before 1950. Since this date, a change in the minimum mesh size, expansion of the fishing grounds and differences in the quality of available data have necessitated a subdivision of the period into three phases: 1950–1963, 1964–1972 and 1973–1976. Each of these was treated in a separate manner.

1950 – 1963

The prescribed minimum mesh size of treated cotton nets in use from 1950 to 1955 was 38 mm, but the gap was rapidly reduced by shrinkage to an average of 32 mm. Because of this, 32 mm was adopted as the new minimum when synthetic nets were introduced in 1956 and can for most purposes be regarded as the effective minimum for the period 1950 – 1963. During these years, the fishery was almost entirely dependent upon three species – pilchard, horse mackerel and mackerel.

Fishing operations were initially confined to the environs of St Helena Bay but later expanded southwards. Davies (1956) recorded that 92 per cent of all catches made from 1950 to 1955 were located between Lambert's Bay and

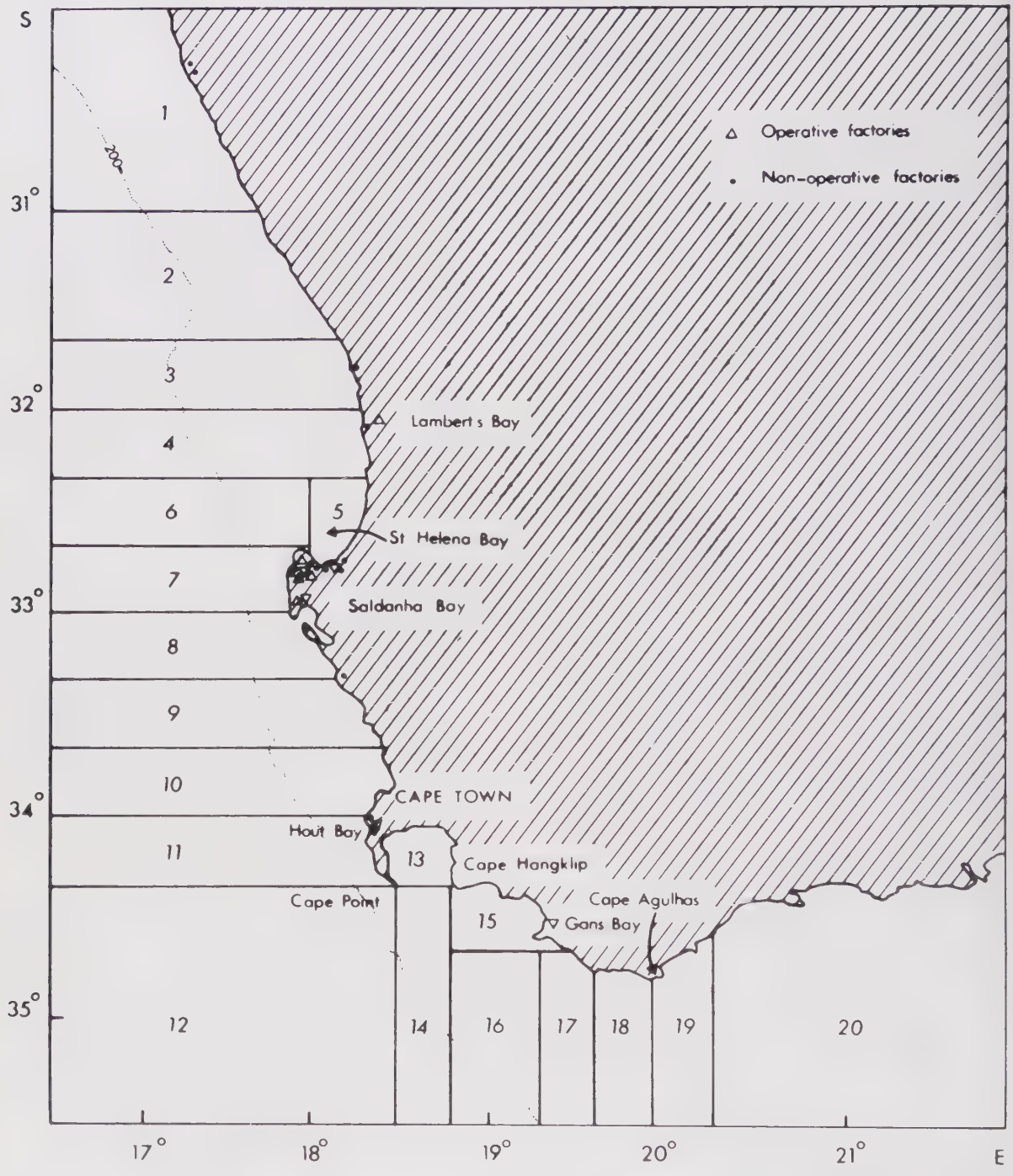


Fig. 1: Factories and fishing grounds of the Western Cape purse-seine fishery showing the 20 areas used in the analysis

St Helena Bay, but by the end of 1958 the area of exploitation extended from Lambert's Bay to Cape Hangklip (Du Plessis 1959). In January 1959, two new reduction plants were opened at Hout Bay in order to make more effective use of the southern concentrations of fish, and were followed in January 1963 by one at Gans Bay.

Skipper reports only commenced in 1956 and until 1963 were irregular and incomplete, so factory estimates of the species composition of the catches were accepted. These are thought to be largely accurate, as field sampling indicated that landings involving more than one species were infrequent. It is possible that catches of round herring were wrongly classified as pilchard on occasion. From 1964 to 1972, 65 per cent of the round herring catch came from waters between Saldanha Bay and Cape Point (Centurier-Harris and Crawford 1974). Any misidentification of the catches is therefore likely to have been severest after fishing had been extended to these waters.

Length-frequency information was collected at Lambert's Bay (1950–1953), St Helena Bay (1950–1963) and Hout Bay (1960–1963). At all localities, samples of 50 fish each were taken from one boat on each day that fish were landed, after tests had indicated that there was little advantage to be had from sampling more vessels. The data intake at Lambert's Bay was terminated after comparison with samples obtained at St Helena Bay had revealed no significant difference (Davies 1957).

The length information was grouped on a monthly basis and combined with factory estimates of species catch to obtain annual age compositions. The age-length keys used in this process are tabulated in the Appendix. In the case of pilchard and mackerel, it was necessary to adopt age data procured at a later date, and estimates may be biased if there were discrepancies in growth rates between the respective periods.

Pilchard scales were collected from 1950 to 1963 and were used by Davies (1958) in a preliminary age study. However, later analysis showed the results obtained from scales to be at variance with those recorded from otoliths in 30 per cent of the comparisons and as, in the cases of pilchard, rings are more clearly defined on otoliths (Baird 1970), scale readings were rejected. Age determination from otoliths has been described by Baird (*op. cit.*) for pilchard, Geldenhuys (1973) for horse mackerel, Baird (1974) for mackerel and Geldenhuys (in press) for round herring, and from scales by Pollock (1970) for anchovy. In contrast to pilchard, anchovy otoliths are extremely difficult to interpret.

1964 – 1972

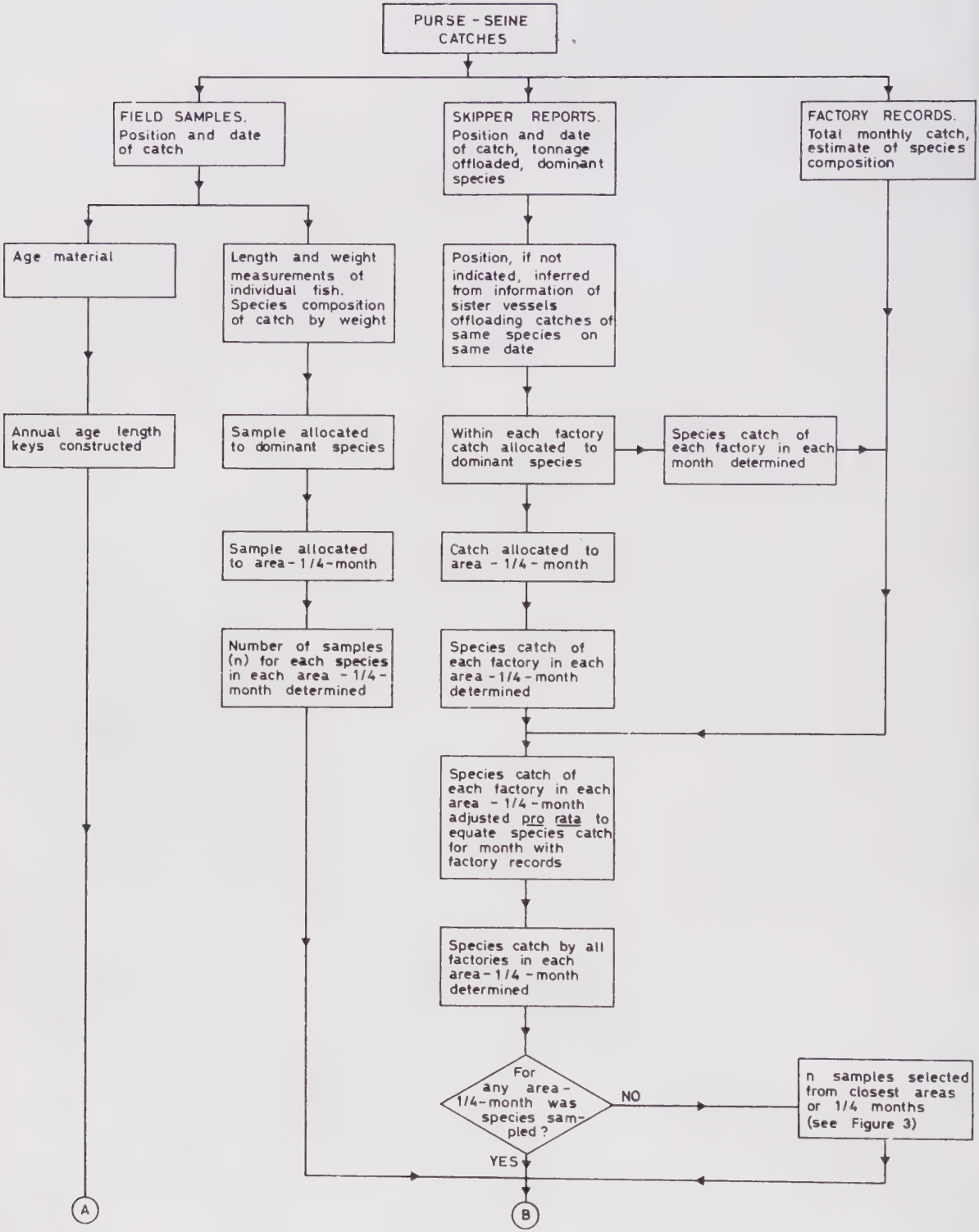
In 1964, certain boats were permitted to fish for anchovy with nets having a minimum mesh size of 12,7 mm. The experiment proved successful and from the beginning of the 1965 season this concession was extended to all vessels. In these two years no other species were allowed to be caught with the small-meshed nets, but difficulties were experienced in identifying shoals before the nets were set, and from 1966 the exploitation of all species with the 12,7 mm net was sanctioned. This lowering of the minimum mesh size had a marked impact on the fishery. Landings of anchovy and round herring increased considerably and the age structures of the pilchard, horse mackerel and mackerel catches were lowered. Lantern-fish made its first documented appearance in 1966, but was only recorded separately from anchovy during 1968 and subsequently.

The abundance of large pilchard on the fishing grounds off the West Coast declined at this time and led to increased fishing east of Cape Point, particularly from January to April. This was facilitated by the introduction of larger fishing vessels with an extended range, allowing many of the boats from Lambert's Bay, Saldanha Bay and St Helena Bay to fish on the southern grounds and also as far north as the Orange River.

In 1964, skipper reports accounted for 55 per cent of the total catch (Table I). The coverage

Table I: Percentage of the total catch reported by the skippers

Year	Reported catch (metric tons)	Actual landings (metric tons)	Percentage reported
1964	233 288	425 622	54,8
1965	288 992	480 129	60,2
1966	300 112	357 134	84,0
1967	491 898	509 313	96,6
1968	368 939	368 593	100,0
1969	349 651	351 951	99,3
1970	356 354	358 886	99,3
1971	326 784	324 531	100,0
1972	433 666	433 597	100,0
1973	408 151	451 393	90,4
1974	383 871	400 499	95,8
1975	351 929	407 415	86,4
1976	358 700	407 545	88,0


PURSE - SEINE CATCHES
FIELD SAMPLES. Position and date of catch
SKIPPER REPORTS. Position and date of catch, tonnage offloaded, dominant species
FACTORY RECORDS. Total monthly catch, estimate of species composition
Age material
Length and weight measurements of individual fish. Species composition of catch by weight
Position, if not indicated, inferred from information of sister vessels offloading catches of same species on same date
Annual age length keys constructed
Sample allocated to dominant species
Within each factory catch allocated to dominant species
Species catch of each factory in each month determined
Sample allocated to area - 1/4 - month
Catch allocated to area - 1/4 - month
Number of samples (n) for each species in each area - 1/4 - month determined
Species catch of each factory in each area - 1/4 - month determined
Species catch of each factory in each area - 1/4 - month adjusted pro rata to equate species catch for month with factory records
Species catch by all factories in each area - 1/4 - month determined
For any area - 1/4 - month was species sampled ?
NO
n samples selected from closest areas or 1/4 months (see Figure 3)
YES
A
B

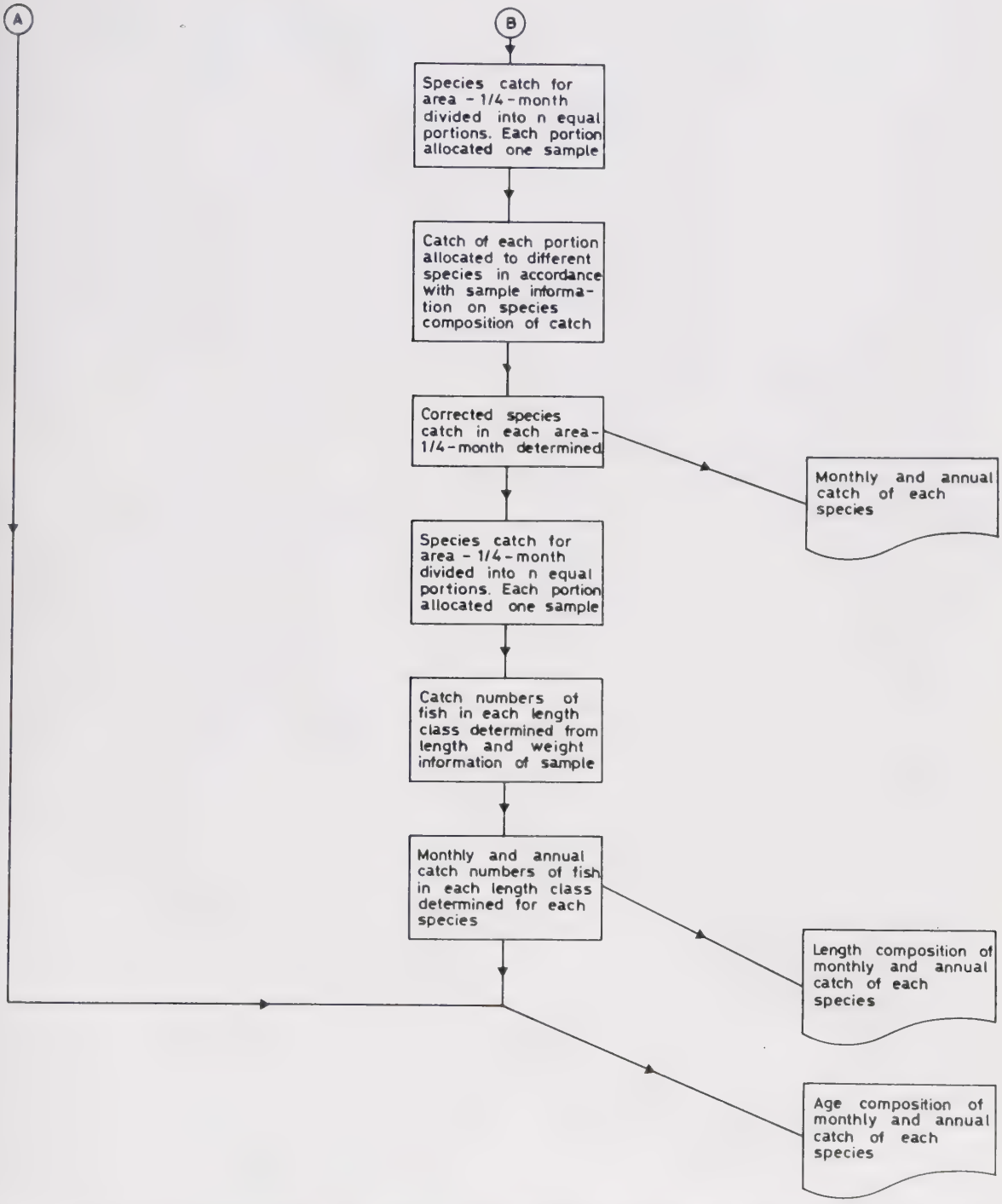

A
B
Species catch for area – 1/4 – month divided into n equal portions. Each portion allocated one sample
Catch of each portion allocated to different species in accordance with sample information on species composition of catch
Corrected species catch in each area – 1/4 – month determined
Monthly and annual catch of each species
Species catch for area – 1/4 – month divided into n equal portions. Each portion allocated one sample
Catch numbers of fish in each length class determined from length and weight information of sample
Monthly and annual catch numbers of fish in each length class determined for each species
Length composition of monthly and annual catch of each species
Age composition of monthly and annual catch of each species

Fig. 2: Diagrammatic representation of the method of treating data for the period 1964 – 1972 to compute the revised monthly and annual catch and age composition of species contributing to the Western Cape purse-seine fishery

continued to improve and was almost complete by 1967. Between 1964 and 1972, the total catch, dominant species and catch position of each trip were recorded, but from 1973 estimates of the species composition of each landing also became available. For this reason the periods 1964–1972 and 1973–1976 have been treated separately, though in both instances the fishing grounds were divided into 20 areas (Fig. 1), following a preliminary division into 28 areas (Centurier-Harris and Crawford 1974).

During the years 1964–1972 the species catch of each factory in each area was determined from skipper returns for each quarter month. These values were then adjusted *pro rata* to ensure that the total catch of each species in every month corresponded to the official factory figures. This process led to a first approximation of the species composition of the catches and also accounted for those catches for which no skipper returns had been received.

The final species breakdown was obtained by adjusting the catch of each species in each area-quarter-month according to field observations for that same locality in time and space. Sampling during the period was conducted at St Helena Bay (1964–1971), Saldanha Bay (1972), Hout Bay (1964–1972) and Gans Bay (1972). The sample size was increased in 1972 to approximately 150 fish. When no field information was available for any particular area-quarter-month, data from the nearest space-time intervals were employed. This involved a search routine in which a computer scanned adjacent and progressively further removed areas and quarter-month intervals (Fig. 3).

Once this process had been completed, length distributions were computed in a similar manner, that is from field data for the area-quarter-month associated with or closest to the catch locality. These length distributions were then used to generate the monthly and annual age structures of the catches. The age-length keys used in this analysis appear in the Appendix. They were all constructed from age material collected during the period, but the data were generally insufficient to provide separate keys for individual years, and any inter-year difference in growth would not have been accounted for.

The entire weighting procedure for the period 1964 to 1972 is illustrated in Figure 2.

1973 – 1976

Skipper estimates of the species composition of catches during this period obviated the necessity of using factory figures to obtain a first approximation of the landings, though adjustments were still made to account for unreported catches. Otherwise the techniques employed were the same as those for 1964 – 1972. Samples of all species were collected from Lambert's Bay (1976), Saldanha Bay (1973–1976), Hout Bay (1973–1976) and Gans Bay (1973–1976), and of mackerel only from St Helena Bay (1973 and 1974). The intake of age material was intensified, with the result that annual keys were available for pilchard and biennial keys for mackerel and round herring. These are listed in the Appendix. Age data from the previous period were employed for anchovy and horse mackerel.

DISCUSSION

An analysis of the searching process, in the event of samples being unavailable for a particular area-quarter-month interval, is presented in Table II. The number of intervals having no samples of their own fell by half, from 89 per cent in 1964 to 44 per cent in 1976, when regular field observations were obtained from four localities for the first time.

The opening of a field station at Gans Bay in 1972 had little impact on the overall picture, probably because this year also witnessed the closure of the St Helena Bay field station in favour of one at Saldanha Bay. As a result, the increased sampling of catches from the eastern fishing grounds was largely offset by a reduced coverage of the northern areas. This deficiency led to the reopening of the Lambert's Bay station in 1976. The relatively high values for negative sampling of 60 and 66 per cent in 1973 and 1974 respectively were probably due to the early end of the fishing season in these two years, the equivalent amount of fish being caught in a shorter period of time and so allowing less opportunity for sampling.

Table II also indicates the extent to which searching took place. When samples were adopted from other areas they almost invariably came from the nearest five areas on either side, that is within a range of about 185 km, and were frequently from the adjacent areas. Similarly it was seldom necessary to employ information from intervals displaced by more than five quarter-months. The 1964 season was an exception, suggesting that sampling during this year

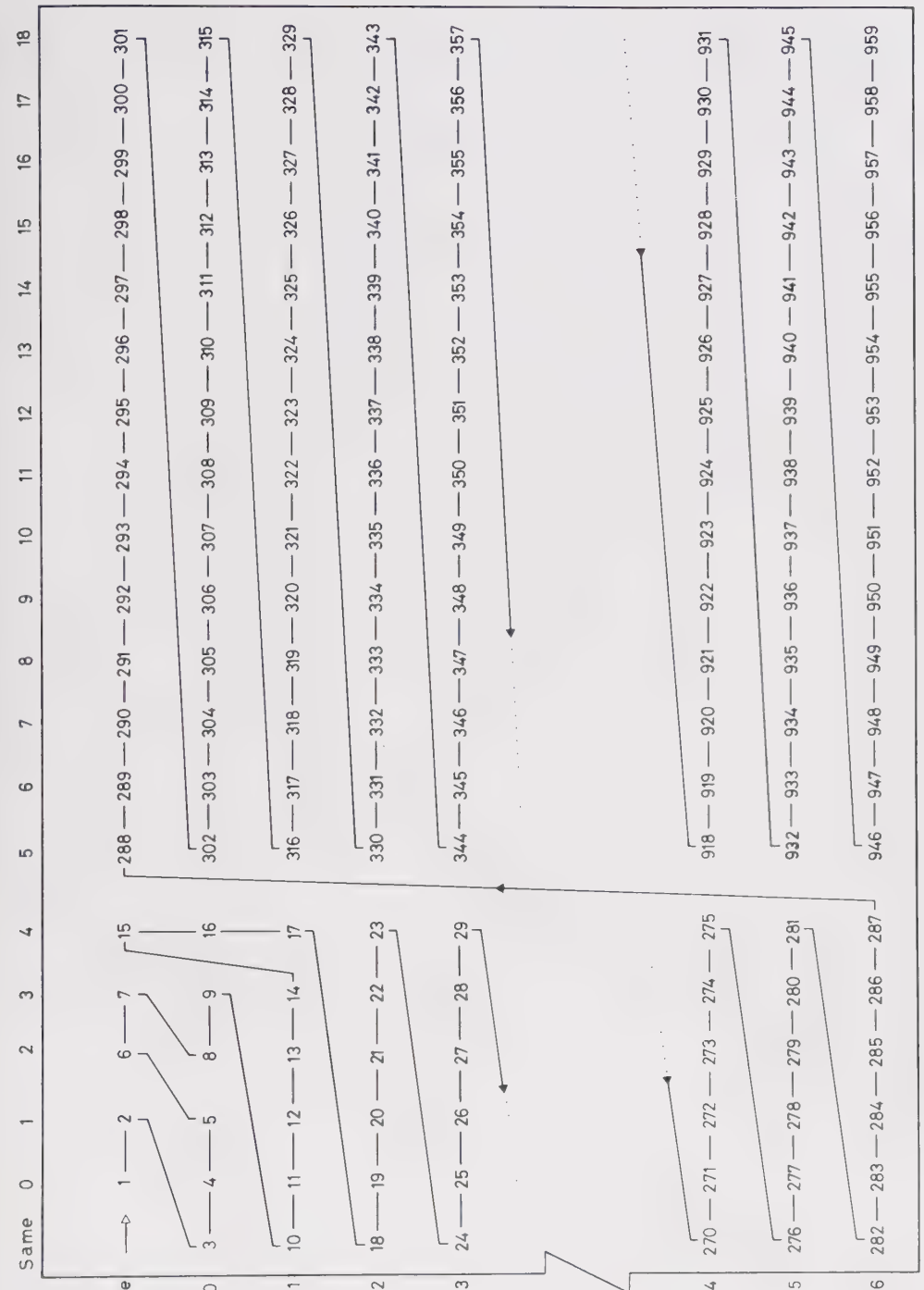


Fig. 3: Computer scanning routine used to find samples when none were available for a particular area-quarter-month. The number of steps required to reach each search level is indicated

Table II: Percentage of all area-quarter-months for which samples were derived from other space-time intervals

Year	Percentage of all area-quarter-months with							
	no sample	sample derived from						
		other areas when number of intervening areas was				other quarter months when number of intervening quarter months was			
		0	1	2–4	>4	0	1	2–4	>4
1964	89,1	21,4	17,8	28,6	1,0	19,7	6,3	8,5	21,3
1965	65,8	24,3	15,4	13,9	1,0	26,0	7,5	3,6	0,5
1966	56,9	23,0	12,9	11,1	0,2	19,0	7,5	3,6	1,4
1967	58,6	18,7	11,0	19,3	1,9	14,7	5,9	9,4	7,8
1968	48,9	15,5	12,5	13,7	0,0	13,9	4,3	6,0	4,0
1969	44,5	14,8	10,3	13,5	1,0	12,6	3,8	6,8	1,7
1970	51,1	16,3	13,0	11,5	4,5	14,3	5,5	4,6	5,3
1971	53,6	15,7	12,0	17,8	0,1	17,2	8,5	7,6	4,0
1972	53,5	16,5	11,6	15,3	3,1	16,0	7,2	4,0	2,5
1973	60,0	19,4	14,0	15,9	2,6	20,1	2,9	7,3	8,8
1974	66,2	23,8	16,8	15,5	4,3	14,8	6,8	7,3	8,8
1975	51,7	18,7	11,7	14,3	0,0	15,0	5,5	7,6	0,8
1976	43,5	22,5	10,1	8,2	0,2	6,5	2,9	2,5	2,4

was relatively inadequate. In extreme instances, data were selected from intervals as far removed as 16 areas or 42 quarter-months and under such circumstances any estimate of the length distribution, or species or age composition of the catch would have been little more than a necessary guess.

In a limited number of cases, additional information on the average weight of anchovy caught in area-time intervals having no sample of their

Table III: Species composition of South African purse-seine fish landings, 1950 – 1976 (thousands of metric tons)

Year	Pilchard	Anchovy	Horse mackerel	Mackerel	Round herring	Lantern-fish	Total
1950	85,3	—	49,9	—	—	—	135,2
1951	101,9	—	98,5	—	—	—	200,4
1952	170,0	—	102,6	—	—	—	272,6
1953	132,5	—	85,2	—	—	—	217,7
1954	88,3	—	118,1	4,0	—	—	210,5
1955	121,9	—	78,8	20,2	—	—	221,0
1956	76,6	—	45,8	32,6	—	—	154,9
1957	109,5	—	84,6	7,4	—	—	201,5
1958	194,4	0,2	56,4	21,6	0,8	—	273,4
1959	260,2	1,4	17,7	33,1	2,6	—	314,9
1960	318,0	—	62,9	31,0	0,1	—	412,0
1961	402,2	—	38,9	49,7	0,1	—	490,9
1962	410,2	—	66,7	20,4	0,1	—	497,3
1963	390,1	0,3	23,2	13,2	0,2	—	427,0
1964	256,1	92,4	24,4	50,0	2,7	—	425,6
1965	204,5	171,0	55,0	41,4	8,2	—	480,1
1966	118,0	143,9	26,3	53,4	15,4	—	357,1
1967	69,7	270,6	8,8	128,2	32,0	—	509,3
1968	107,8	138,1	1,4	91,0	30,3	0,1	368,6
1969	56,1	149,2	26,8	91,7	23,3	4,9	352,0
1970	61,8	169,3	7,9	77,9	23,7	18,2	358,9
1971	87,6	157,3	2,2	54,2	21,6	2,0	324,9
1972	104,2	235,6	1,3	56,7	20,6	15,2	433,6
1973	69,0	250,9	1,6	58,8	28,7	42,4	451,4
1974	16,0	349,8	2,5	30,7	1,3	0,3	400,5
1975	89,2	223,6	1,6	69,3	23,6	0,1	407,4
1976	176,4	218,3	0,4	0,5	11,7	0,1	407,5

Table IV: Age composition of the South African pilchard landings, 1950 – 1976 (thousands of fish caught)

Year	Age class								
	O	I	II	III	IV	V	VI	VII	VIII
1950			4 420	64 240	176 370	221 820	146 290	24 020	870
1951		70	4 650	44 000	209 720	280 240	169 170	27 450	860
1952	670	4 160	19 510	224 330	475 460	436 280	206 240	23 350	530
1953	270	3 790	26 590	87 400	336 620	391 180	175 370	19 080	480
1954			310	24 140	204 450	281 150	131 920	9 230	250
1955			50	22 430	261 140	403 030	187 460	12 120	240
1956	420	4 010	9 000	45 200	139 900	224 630	134 220	11 490	160
1957	50	3 240	62 480	174 350	290 230	271 100	123 060	18 220	150
1958			112 590	1 070 740	650 670	207 930	58 940	5 860	60
1959	1 700	26 890	412 690	1 719 110	927 360	156 130	8 670	250	
1960	1 030	14 900	323 030	1 714 270	1 299 950	291 110	16 530	250	
1961	90	2 400	77 040	827 460	1 902 910	847 160	102 090	1 280	
1962		1 220	163 570	1 304 660	1 651 060	768 130	140 200	350	
1963	16 190	117 640	838 750	1 233 910	1 526 760	681 780	92 980	740	
1964	790	12 540	252 208	1 080 797	918 121	203 871	21 014	414	
1965	234 643	129 479	317 600	1 027 346	599 248	155 792	14 788	125	
1966	370 269	73 554	55 361	404 675	411 697	150 764	17 326		
1967	3 623 027	812 973	108 490	156 079	56 258	6 984	122		
1968	4 306 589	643 292	158 907	354 231	197 605	43 870	3 270		
1969	2 558 093	326 484	203 627	254 937	53 721	7 363	136		
1970	1 631 633	421 336	192 776	356 778	60 138	3 154			
1971	4 489 153	682 438	164 127	296 736	87 793	8 172	211		
1972	1 317 150	686 689	203 829	201 560	216 383	76 619	12 784		
1973	3 010 414	14 215	179 492	187 765	25 895	1 166	50		
1974		48 296	16 991	49 685	52 664	18 207	3 853		
1975	2 688 417	466 480	172 837	186 029	99 663	34 407	1 261		
1976	10 172	429 148	1 232 342	741 651	124 735	12 373	367		

own was available and, when compared with the adopted samples, indicated that a biased picture was being presented. The majority of such comparisons, however, validated the allocation process, and the scarcity of occasions on which searching extended to distant intervals suggests that the method is superior to the former process of lumping all information on an annual basis.

Table V: Age composition of the South African anchovy landings, 1964–1976 (thousands of fish caught)

Year	Age class				
	O	I	II	III	IV
1964	4 112 558	3 691 963	1 032 013	264 526	25 809
1965	6 112 724	5 888 132	2 552 185	846 577	106 995
1966	17 472 147	3 755 349	876 426	262 574	24 167
1967	31 844 250	8 111 306	1 299 942	518 433	104 438
1968	13 352 969	4 810 371	701 545	226 698	41 462
1969	18 344 074	4 313 846	612 167	158 040	19 940
1970	24 597 890	4 522 904	830 006	208 994	26 982
1971	12 822 676	5 463 940	1 192 470	485 286	70 238
1972	10 107 668	7 417 308	1 619 056	655 910	121 340
1973	28 878 896	3 593 843	139 651	16 107	7
1974	19 302 169	12 619 213	1 972 432	312 830	8 299
1975	28 793 310	5 229 766	1 355 714	277 282	10 025
1976	18 775 756	7 474 908	1 097 631	202 036	18 098

Revised catch figures for the period 1950–1976 are presented in Table III, whereas annual age compositions for the landings of all species except lantern-fish appear in Tables IV to VIII. Comparison with previously published figures (Baird 1975, Baird and Geldenhuys 1973, Sea Fisheries Branch 1950–1974) shows that since 1966, when legislation first provided for the capture of all species with the small-meshed net, the adjustment of catch figures to take into account the effect of mixed catches has resulted in significant changes. After this date, former figures usually underestimated the catches of pilchard and round herring, while overestimating those of anchovy. This was because anchovy was generally the main contributor in mixed catches involving these three species.

The 1974 season proved to be a notable exception, there being very little change in species catch. In this year, juveniles of both pilchard and round herring were noticeably absent from the catches, with the result that mixed catches were seldom encountered. The close correlation between the former and revised catch totals in this year suggests that figures for the period

Table VI: Age composition of the South African horse mackerel landings, 1950–1976 (thousands of fish caught)

Year	Age class												
	O	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
1950			50 000	213 000	58 800	19 100	24 200	8 570	8 570	1 950	3 120	2 340	
1951			8 030	164 000	114 000	116 000	68 000	31 600	19 800	2 680	5 350	5 890	
1952	15 100	45 900	3 910	23 000	62 100	173 000	85 500	54 700	12 700	1 950	2 930	7 330	
1953				11 500	19 000	84 600	54 000	65 600	26 600	2 120	3 930	5 140	
1954			3 220	10 400	14 300	53 700	88 500	73 400	78 100	7 520	14 300	14 000	358
1955				922	2 770	45 600	58 500	51 900	34 800	16 600	9 220	9 220	922
1956				344	2 180	10 400	17 800	24 900	23 600	15 500	14 700	3 780	1 600
1957			2 900	17 400	4 840	13 000	16 300	28 500	39 500	26 500	41 000	10 800	8 520
1958			623	2 740	5 360	8 970	7 470	9 970	27 200	16 300	22 800	14 500	5 980
1959			240	2 160	5 660	8 440	6 380	3 020	4 320	4 840	7 620	3 360	1 970
1960		510	16 600	27 300	41 500	74 400	42 300	8 410	9 170	4 330	17 100	8 920	4 330
1961			177	8 300	29 500	76 500	52 300	5 470	1 770			706	1 770
1962			234	1 870	16 600	58 100	101 000	25 100	16 900	1 870	5 160	5 160	2 110
1963	No data available												
1964			16 553	56 720	48 481	45 391	9 306	6 548	809				
1965	29 586	6 760	43 396	58 731	97 417	56 997	8 330	8 937	517	14	14		
1966	166 818	80 608	22 205	19 345	36 549	27 307	4 150	4 805	803	33	58		
1967	16 842	47 336	122 694	7 022	575								
1968	32 954	1 767	4										
1969	125 150	28 205	10 718	18	506	14 558	15 430	11 947	10 699	3 210	2 063		
1970	688 380	124 028	3 556										
1971	57 647	3 835	3 041	62	49	14							
1972			1 205	5 420	4 452	1 118							
1973	38 015		557	1 646	3 075	1 896	290	408					
1974	140 376	26 415	4 149										
1975	No data available												
1976	No data available												

Table VII: Age composition of the South African mackerel landings, 1954–1976 (thousands of fish caught)

Year	Age class								
	O	I	II	III	IV	V	VI	VII	VIII
1954	62	410	1 972	1 290	310	8			
1955		902	8 757	6 383	2 234	46			
1956	2	2 912	18 024	7 033	3 034	663	248	45	6
1957				290	1 107	879	679	182	41
1958	701	26 308	20 120	1 321	3				
1959	6	7 708	30 125	6 211	175				
1960	589	7 340	13 813	10 109	2 627	72			
1961	6	9 095	42 430	9 661	1 194	67			
1962		680	10 664	6 332	1 194	59	11	2	
1963	40 070	7 469	10 845	1 129					
1964	33 001	109 334	12 312	69					
1965	71	2 204	7 753	7 060	4 323	531	58	9	
1966	252 636	1 120	16 179	9 415	1 496	51	6		
1967	312 501	293 427	8 871	2 866	288	20			
1968	3 622	48 632	51 639	13 291	7 787	1 492	373	61	4
1969	21 225	17 974	34 095	14 020	12 014	3 229	1 199	228	39
1970	9 512		789	9 584	16 838	6 012	2 385	442	41
1971	39 694	16 242	15 032	6 344	5 089	1 819	781	152	9
1972	8 135	44 632	32 995	8 764	1 064	292	140	53	17
1973	64	11 687	60 458	8 626	1 099	125			
1974	39 792	1 225	24 130	4 440	138				
1975	366	55 299	32 124	17 614	2 269	298	27		
1976	431	945	155	1					

Table VIII: Age composition of the South African round herring landings, 1964–1976 (thousands of fish caught)

Year	Age class						
	O	I	II	III	IV	V	VI
1964	34	9	18 823	18 222	2 907	243	
1965	6 567	4 512	20 852	38 902	12 465	1 863	
1966	290 346	253 304	46 817	32 620	7 792	732	
1967	1 085 828	441 715	65 807	139 111	61 433	12 493	
1968	4 198 734	635 560	96 674	85 291	23 868	3 173	
1969	2 553 906	422 729	32 889	65 480	32 230	6 713	
1970	2 773 755	844 905	139 338	23 601	3 453	218	
1971	406 855	293 368	92 152	89 191	28 606	3 345	
1972	93 596	13 121	65 125	122 543	52 006	2 419	
1973	226 920	140 102	73 740	192 466	53 423	1 975	
1974	2 289	18 710	7 635	6 614	1 719	76	
1975	982 082	171 246	77 740	178 215	47 776	5 276	316
1976	660 106	403 788	47 763	24 854	8 083	1 458	207

1950–1963, when no correction was introduced to account for mixed landings, are reasonably accurate.

ACKNOWLEDGEMENTS

The authors wish to thank Messrs H. G. v. D. Boonstra and A. I. L. Payne for their helpful comments on the manuscript which resulted in considerable improvement. Mr S. R. da F. Baptista contributed the artwork, and Dr G. G. Newman provided much encouragement during the revision of the data.

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APPENDIX

Age-length keys used in the weighting procedure

In each case, the length class Lc (cm) given refers to the mean of each 0,5-cm or 1-cm length group (e.g. 12,75 cm refers to fish 12,50 – 12,99 cm in Lc).

Lc is the length from the tip of the snout to the tip of the caudal peduncle.

PILCHARD

Period of use: 1950–1971
Age material collected: 1965–1967

Length class Lc (cm)	Age class										Total
	0	I	II	III	IV	V	VI	VII	VIII	IX	
5,25	3										3
5,75	5										5
6,25	2										2
6,75	11										11
7,25	14										14
7,75	14										14
8,25	15										15
8,75	18	1									19
9,25	33	4									37
9,75	19	3									22
10,25	18	7									25
10,75	20	12									32
11,25	15	13									28
11,75	12	20									32
12,25	3	24	1								28
12,75		17	1								18
13,25	3	13	4								20
13,75	1	9	12								22
14,25		4	14	1							19
14,75		2	18	3							23
15,25		1	13	4							18
15,75			5	8							13
16,25			3	8							11
16,75			4	10							14
17,25			4	11	1						16
17,75			4	11	3						18
18,25			2	17	3						22
18,75			3	23	4	1					31
19,25			2	35	13	1					51
19,75			1	24	17						42
20,25				7	23	2					32
20,75				2	26	9					37
21,25				2	14	8	1				25
21,75				2	12	9					23
22,25					7	18	4				29
22,75					4	8	6				18
23,25					3	8	7				18
23,75					1	8	8	1			18
24,25						4	8	4			16
24,75						1	8	6			15
25,25						1	8	8	1		18
25,75							4	8	4		16
26,25							1	8	6		15
26,75							1	8	8	1	18
Total	206	130	91	168	131	78	56	43	19	1	923

PILCHARD

Period of use: 1972
Age material collected: 1972

Length class Lc (cm)	Age class							Total
	0	I	II	III	IV	V	VI	
8,25	13							13
8,75	12							12
9,25	37	4						41
9,75	25	2						27
10,25	43	11						54
10,75	34	8						42
11,25	51	15						66
11,75	53	28	1					82
12,25	50	32	5					87
12,75	30	42	6					78
13,25	17	31	4	1				53
13,75	13	14	3					30
14,25		8	8	1				17
14,75		11	21	7				39
15,25		5	26	9				40
15,75		6	36	21				63
16,25		6	45	18	5	1		75
16,75		8	27	26	8	1		70
17,25		3	27	36	16	4		86
17,75			16	31	36	15		98
18,25			6	40	45	16	4	111
18,75			9	33	50	11	3	106
19,25			1	16	65	29	3	114
19,75			1	7	31	13	3	55
20,25				4	6	7	2	19
20,75					2	3	1	6
21,25				1	15	8	1	25
21,75					12	9	1	22
22,25					5	16	2	23
22,75					4	7	6	17
23,25					2	4		6
23,75						1		1
Total	378	234	242	251	302	145	26	1 578

Period of use: 1973
Age material collected: 1973

Length class Lc (cm)	Age class							Total
	0	I	II	III	IV	V	VI	
6,25	2							2
6,75	3							3
7,25	5							5
7,75	4							4
8,25	1							1
8,75	2							2
9,25	9							9
9,75	9							9
10,25	3							3
10,75	1							1
11,25	1							1
11,75	2	1						3
12,25		1	3					4
12,75		3	1					4
13,25		3	1					4
13,75		4						4
14,25		4	5	1				10
14,75		2	14	4				20
15,25		1	11	4				16
15,75			15	5				20
16,25		1	7	5				13
16,75			11	9				20
17,25		1	27	30				58
17,75		1	42	35				78
18,25			58	40	1			99
18,75			49	47	3			99
19,25			40	44	3			87
19,75			16	49	17			82
20,25			12	30	21	2		65
20,75			7	25	8	1		41
21,25				1	7	4	1	13
21,75				1	6	5		12
22,25					2	8	1	11
22,75					2	4	3	9
23,25					2	4		6
23,75						2		2
Total	42	22	319	330	72	30	5	820

PILCHARD

Period of use: 1974
Age material collected: 1974

Length class Lc (cm)	Age class 0	I	II	III	IV	V	VI	Total
10,25		1						1
10,75		1						1
11,25		2						2
11,75		1						1
12,25		1						1
12,75		1						1
13,25		1						1
13,75		1						1
14,25		2	2					4
14,75		1	1	1				3
15,25		2	3	2				7
15,75		2	4	1				7
16,25		2	4	3				9
16,75		1	10	23	4			38
17,25			17	25	10			52
17,75			9	38	25	2		74
18,25			14	34	26	8		82
18,75			12	48	35	10	2	107
19,25			15	36	52	18	3	124
19,75			7	42	53	19	4	125
20,25			2	23	40	19	6	90
20,75			2	16	52	24	4	98
21,25				4	27	10	3	44
21,75				3	15	12	2	32
22,25					3	3	6	12
22,75					5	17	2	24
23,25					2	3	3	8
23,75					1	2		3
24,25						2		2
Total		19	100	299	350	149	35	954

Period of use: 1975
Age material collected: 1975

Length class Lc (cm)	Age class 0	I	II	III	IV	V	VI	Total
9,25	4							4
9,75	2							2
10,25	16	4						20
10,75	14	11						25
11,25	17	18						35
11,75	8	18						26
12,25	4	6	2					12
12,75		2	3					5
13,25		6	2					8
13,75		4	2					6
14,25		3	3					6
14,75			4					4
15,25		1	12					13
15,75			20					20
16,25		3	41	11	3			58
16,75		5	56	8	3			72
17,25		2	80	26	6			114
17,75			81	29	6			116
18,25			56	46	18	6		126
18,75			33	71	18	2		124
19,25			6	80	36	13		135
19,75			7	62	46	18		133
20,25			1	45	51	23		120
20,75				24	64	23	2	113
21,25			1	13	32	17	4	67
21,75				2	12	8	4	26
22,25					10	34	4	48
22,75					8	14	12	34
23,25					3	6		9
23,75						1		1
Total	65	83	410	417	316	165	26	1 482

Period of use: 1976
Age material collected: 1976

Length class Lc (cm)	Age class 0	I	II	III	IV	V	VI	Total
9,25		3						3
9,75		3						3
10,25		10						10
10,75		8						8
11,25		8	1					9
11,75		8	3					11
12,25		8	2					10
12,75		9	2					11
13,25		18	4					22
13,75		19	7					26
14,25		25	9	2				36
14,75		20	21	3				44
15,25		23	29	6				58
15,75		7	54	12				73
16,25		3	63	29	2			97
16,75		3	71	28	2			104
17,25		1	47	53	5			106
17,75		1	35	38	7			81
18,25			27	39	18			84
18,75			13	19	3	1		36
19,25			4	17	4	1		26
19,75			3	4	6	4		17
20,25				6	9	2		17
20,75					11	2		13
21,25					2	2	1	5
21,75					3			3
Total		177	395	256	72	12	1	913

ANCHOVY

Period of use: 1964 – 1976
Age material collected: 1965 – 1967

Length class Lc (cm)	Age class					Total
	0	I	II	III	IV	
6,75	3					3
7,25	8					8
7,75	17	1				18
8,25	30	2				32
8,75	33	8				41
9,25	35	14				49
9,75	24	25				49
10,25	5	28	5			38
10,75	6	26	7	2		41
11,25	1	22	29	3		55
11,75		10	18	7		35
12,25		1	17	13	2	33
12,75			7	12	5	24
13,25			1	6	2	9
13,75				4	2	6
14,25				2	2	4
Total	162	137	84	49	13	445

HORSE MACKEREL

Period of use: 1950 – 1962
Age material collected: 1950 – 1965

Length class Lc (cm)	Age class												Total
	0	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	
4,50	1												1
5,50													
6,50	9												9
7,50	7												7
8,50	18	2											20
9,50	5	6	1										12
10,50		5											5
11,50		3	3										6
12,50		1	4										5
13,50		1	3										4
14,50			5										5
15,50			4	1									5
16,50			4	4									8
17,50			5	5	2								12
18,50			1	6	1								8
19,50			1	9	7	3							20
20,50				4	8	2							14
21,50				7	4	9	3						23
22,50				1	7	11	3						22
23,50				1	16	22	5	3					47
24,50				1	2	13	4	3					23
25,50					1	9	13	1	6				30
26,50					1	8	17	10	5				41
27,50						4	12	11	1				28
28,50						2	11	7	4		1		25
29,50							4	4	2	1	1		12
30,50							1	4	1	1			7
31,50							1	4	4		4		13
32,50								2	2	2	5	1	12
33,50										2	2	1	5
34,50								1	3	1	2		7
35,50									1		4		5
36,50													
37,50											1		1
38,50													
Total	40	18	31	39	49	83	74	50	29	7	20	2	442

HORSE MACKEREL

Period of use: 1964 – 1974
Age material collected: 1965 – 1969

Length class Lc (cm)	Age class											Total
	0	I	II	III	IV	V	VI	VII	VIII	IX	X	
6,50	9											9
7,50	10											10
8,50	6	2										8
9,50	18	9	1									28
10,50		7										7
11,50		4	2									6
12,50		2	6									8
13,50		2	3									5
14,50		1	2									3
15,50			11									11
16,50			3	2								5
17,50			3	3								6
18,50				5	1							6
19,50				1	3	1						5
20,50			1		6	1						8
21,50				3	6	3	1					13
22,50			1	2	1	2		1				7
23,50				1	4	6	1					12
24,50				1	6	6		2				15
25,50					1	5	1	1	1			9
26,50					1	3	3					7
27,50						3	1	1				5
28,50						2	1	2				5
29,50						1	2					3
30,50								1	2			3
31,50								1		1	1	3
32,50							1	1	2	1		5
33,50									1			1
34,50									1	1	1	3
35,50								1			1	2
36,50									1			1
37,50										1		1
Total	43	27	33	18	29	33	11	11	8	5	3	221

MACKEREL

Period of use: 1954 – 1971
Age material collected: 1968 – 1972

Length class Lc (cm)	Age class									Total
	0	I	II	III	IV	V	VI	VII	VIII	
11,50	5									5
12,50	5									5
13,50	3									3
14,50	1									1
15,50	1									1
16,50	2									2
17,50	10									10
18,50	19									19
19,50	18									18
20,50	22									22
21,50	11									11
22,50	1	1								2
23,50	9	7								16
24,50	21	21								42
25,50	14	23								37
26,50	6	28								34
27,50	8	60	4							72
28,50	8	54	5							67
29,50	1	61	19							81
30,50	1	52	34							87
31,50	1	63	41	1						106
32,50		47	57	5						109
33,50		41	69	10						120
34,50		25	53	6						84
35,50		22	53	7						82
36,50		11	49	7						67
37,50		4	36	7						47
38,50		3	28	4						35
39,50		4	28	9						41
40,50		1	24	7						32
41,50			18	15						33
42,50			11	9	1					21
43,50			9	12	3					24
44,50			7	23	5					35
45,50			1	13	18					32
46,50			2	10	15	1				28
47,50			2	17	23	4				46
48,50				18	34	7				59
49,50				21	29	10	2			62
50,50				11	31	11	5	1		59
51,50				5	23	23	11			62
52,50				4	13	15	7	3		42
53,50					9	7	12	4	1	33
54,50					4	5	7	2	1	19
55,50						1	1			2
56,50							1	2		3
Total	167	528	550	263	208	84	46	12	2	1 818

Period of use: 1972
Age material collected: 1972

Length class Lc (cm)	Age class									Total
	0	I	II	III	IV	V	VI	VII	VIII	
11,50	5									5
12,50	5									5
13,50	3									3
14,50	1									1
15,50	1									1
16,50	2									2
17,50	10									10
18,50	19									19
19,50	18									18
20,50	22									22
21,50	11									11
22,50	1	1								2
23,50	2	4								6
24,50	11	17								28
25,50	11	19								30
26,50	3	21								24
27,50	2	45								47
28,50	1	37								38
29,50		37	3							40
30,50	1	15	13							29
31,50		12	14							26
32,50		6	15	3						24
33,50		4	17	6						27
34,50		8	18	5						31
35,50			10	3						13
36,50			11	3						14
37,50			11							11
38,50			5							5
39,50			2	1						3
40,50			2							2
41,50			2	1						3
42,50			1							1
43,50				3						3
44,50				4						4
45,50				3	1					4
46,50				1	1					2
47,50				1	1					2
48,50					2					2
49,50					2					2
50,50						1				1
51,50					1					1
52,50					2	1				3
53,50					9	7	12	4	1	33
54,50					4	5	7	2	1	19
55,50						1	1			2
56,50							1	2		3
Total	129	226	124	34	23	15	21	8	2	582

MACKEREL

Period of use: 1973 – 1974
Age material collected: 1973 – 1974

Length class Lc (cm)	Age class						Total
	0	I	II	III	IV	V	
11,50	3						3
12,50	4						4
13,50	3						3
14,50	6						6
15,50	11						11
16,50	4						4
17,50	4						4
18,50	7						7
19,50	8						8
20,50	9						9
21,50	11						11
22,50	4	4					8
23,50	9	7					16
24,50	21	21					42
25,50	14	23					37
26,50		2	6				8
27,50		7	10				17
28,50		2	12				14
29,50		3	10				13
30,50		7	21				28
31,50		5	18	2			25
32,50		6	20	2			28
33,50		6	36	6			48
34,50		4	32	5			41
35,50		3	34	11			48
36,50		1	34	9			44
37,50			21	1			22
38,50			22				22
39,50		1	20	3			24
40,50			18	9	1		28
41,50			18	10			28
42,50			22	14	2		38
43,50			9	7	4		20
44,50			3	7	1	1	12
45,50			2	2	3		7
46,50			2	2	2		6
47,50				2	1		3
48,50				2	3		5
49,50					1		1
50,50				2	1	2	5
51,50				1	6		7
52,50				3	4		7
53,50				1	3	1	5
54,50				1	2	1	4
55,50					2		2
Total	118	102	370	102	36	5	733

Period of use: 1975 – 1976
Age material collected: 1974 – 1975

Length class Lc (cm)	Age class							Total
	0	I	II	III	IV	V	IV	
11,50	3							3
12,50	4							4
13,50	3							3
14,50	6							6
15,50	11							11
16,50	4							4
17,50	4							4
18,50	7							7
19,50	8							8
20,50	9							9
21,50	11							11
22,50		3						3
23,50		10						10
24,50		29	1					30
25,50		31	1					32
26,50		35	5					40
27,50		28	4					32
28,50		36	8					44
29,50		40	6					46
30,50		24	14	1				39
31,50		19	13	2				34
32,50		7	6	5				18
33,50		3	7	3				13
34,50		3	5	6				14
35,50		2	11	3				16
36,50		1	18	8				27
37,50			13	5	1			19
38,50			10	9				19
39,50			4	13				17
40,50			1	9				10
41,50				5	3			8
42,50				1	1			2
43,50					1			1
44,50					2			2
45,50				2	2	3		7
46,50				2	2	2		6
47,50					2	1		3
48,50					2	3		5
49,50						1		1
50,50					2	1	2	5
51,50					1	6		7
52,50					3	4		7
53,50					1	3	1	5
54,50					1	2	1	4
55,50						2		2
Total	70	271	127	74	24	28	4	598

ROUND HERRING

Period of use: 1964 – 1971
Age material collected: 1968 – 1972

Length class Lc (cm)	Age class						Total
	0	I	II	III	IV	V	
5,75	14						14
6,25	36	2					38
6,75	57	8					65
7,25	62	14					76
7,75	83	23					106
8,25	48	15					63
8,75	40	23					63
9,25	24	27	1				52
9,75	12	23					35
10,25	11	12	3				26
10,75	3	7					10
11,25	1	12	2				15
11,75		5	6				11
12,25		3	15				18
12,75		3	6				9
13,25		4	8				12
13,75		1	7	1			9
14,25			8				8
14,75			8	2			10
15,25			12	3			15
15,75			19	9			28
16,25			23	15			38
16,75			22	24	2		48
17,25			31	28	3		62
17,75			26	34	7		67
18,25			20	44	10	1	75
18,75			17	41	6		64
19,25			20	42	12	1	75
19,75			9	33	13	1	56
20,25			7	46	20	4	77
20,75			6	29	17	2	54
21,25			1	22	17	5	45
21,75			1	11	9	3	24
22,25				4	7	1	12
22,75				2	4		6
Total	391	182	278	390	127	18	1 386

Period of use: 1972
Age material collected: 1972

Length class Lc (cm)	Age class						Total
	0	I	II	III	IV	V	
6,25	5						5
6,75	5						5
7,25	10						10
7,75	18						18
8,25	9	3					12
8,75	6	1					7
9,25	4	1					5
9,75	5	3					8
10,25	4	1					5
10,75		1					1
11,25	1	12	2				15
11,75		5	6				11
12,25		3	15				18
12,75		3	6				9
13,25		4	8				12
13,75		1	7	1			9
14,25			8				8
14,75			2	1			3
15,25			2	1			3
15,75			5	3			8
16,25			7	3			10
16,75			7	14	1		22
17,25			12	12			24
17,75			5	9	4		18
18,25			4	16	2	1	23
18,75			3	6	3		12
19,25			4	15	2		21
19,75				7	7		14
20,25			1	2			3
20,75			1		1		2
21,25			1	1	1		3
21,75				1	1		2
22,25				2	4	1	7
22,75				1	2		3
Total	67	38	106	95	28	2	336

ROUND HERRING

Period of use: 1973 – 1974
Age material collected: 1973

Length class Lc (cm)	Age class 0	I	II	III	IV	V	Total
5,75	4						4
6,25	10	1					11
6,75	6						6
7,25	8	5					13
7,75	4	5					9
8,25	3	3					6
8,75		6					6
9,25		8					8
9,75		9					9
10,25		1	6				7
10,75		3	1				4
11,25		12	1				13
11,75		5	6				11
12,25		3	15				18
12,75		3	6				9
13,25		4	8				12
13,75		1	7	1			9
14,25			8				8
14,75			8	2			10
15,25		3	17	7			27
15,75		5	27	2			34
16,25		4	38	13			55
16,75		3	35	26			64
17,25			33	49	8		90
17,75			20	65	7		92
18,25			25	52	12	1	90
18,75			12	86	17		115
19,25			10	69	20		99
19,75			8	46	21		75
20,25			2	29	14	2	47
20,75			1	29	18	1	49
21,25				28	12	2	42
21,75			1	11	12		24
22,25				2	4		6
22,75				2	4		6
Total	35	84	295	519	149	6	1 088

Period of use: 1975 – 1976
Age material collected: 1975

Length class Lc (cm)	Age class 0	I	II	III	IV	V	VI	Total
5,75	1							1
6,25	4	1						5
6,75	7	1						8
7,25	9	2						11
7,75	4	1						5
8,25	3	1						4
8,75	7	3						10
9,25	5	6						11
9,75	3	6						9
10,25	4	4	1					9
10,75	6	14						20
11,25		6	1					7
11,75		5	6					11
12,25		1	5					6
12,75		2	4					6
13,25		3	6					9
13,75		1	7	1				9
14,25			6					6
14,75		1	17	2				20
15,25		1	27	19				47
15,75		2	18	31				51
16,25			9	31	2			42
16,75			9	36	1			46
17,25			6	25	8			39
17,75			2	20	4			26
18,25				27	8			35
18,75				17	11			28
19,25				7	18	2		27
19,75				1	19	3		23
20,25				1	15	2		18
20,75					3	8	2	13
21,25						4		4
Total	53	61	124	218	89	19	2	566

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